RECENT ADVANCES IN AGRICULTURAL PLANT BREEDING

BY

H. HUNTER

Hon. M.A. (Cantab.), D.Sc. (Leeds)

Plant Breeding Institute, School of Agriculture, Cambridge

AND

H. MARTIN LEAKE

M.A., Sc.D. (Cantab.)

Formerly Director of Agriculture, United Provinces, India, and Principal of the Imperial College of Tropical Agriculture, Trinidad

WITH A FOREWORD BY

SIR ROWLAND H. BIFFEN, M.A., F.R.S.

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FOREWORD

THE possibilities of improving agricultural plants by cross-breeding had barely been realized at the beginning of this century. It was vaguely recognized that the result of crossing two distinct forms of, say, barley was to " break the type," and the plant breeders' hope was that amongst the numerous forms occurring in the descendants of the cross-breds something better than the parents might be found. If a few plants rewarded their optimism the next task was to " fix the type," generally by a process of mass selection. Failures to do so left the impression in the public mind that hybrid plants always " harked back to the parents," that they were essentially unstable and so of little agricultural value.

Then came the rediscovery of Mendel's Principles of Heredity. The recognition of the independent inheritance of unit characters and of the fact that, by hybridizing, they could be grouped together in fresh combinations laid the foundations of modern plant breeding. Tentative attempts were soon made to test the value for practical purposes of these purely scientific discoveries. It seemed obvious enough, but the question had still to be answered whether characters of agricultural importance such as yield, size, time of maturation, chemical constitution, quality, etc., were inheritable and, if so, on what lines. A direct and positive answer was provided by a number of investigators, though even to this day the precise mode of segregation of some of these vague characters is unknown. It is sufficient for most practical purposes to know that it occurs. The way was then clear some twenty years ago for a systematic attack on the problems of plant improvement.

In the meanwhile the fact has been appreciated that the production of better crops, at no additional expense to the grower, is one of the simplest of methods for adding to a nation's wealth.

As a consequence practically all countries with any claim to be progressive now maintain plant breeding stations for the solution of their own particular crop problems. Russia stands easily at the head of such countries, with numerous stations and a large personnel devoted to the most critical study of the many crops capable of being grown in that country. Moreover, the investigations are not confined to the indigenous forms of these crops, but the world is systematically searched for new forms, not so much in the hope of naturalizing them as in the expectation that they may prove of value to the plant breeders. At the other extreme are to be found some of our colonies with a one-man station, at which the solitary worker concentrates, when the powers that be permit, on some pressing local problem which offers a reasonable chance of solution.

The output of literature is already very considerable and often difficult of access. But the problem of keeping the isolated worker in touch with various branches of his subject and also of the rapidly expanding science of genetics, which is of such great concern to him, has been solved by the abstracting service provided by the Imperial Bureau of Plant Genetics. Few laymen, however, can have any idea of the scope of the work now in progress or even of the nature of the problems to be solved. This book will, for the first time, provide them—and possibly some geneticists who hitherto have paid little attention to the application of their science to everyday life—with it.

Its perusal will show how complex these problems are. Perhaps more often than not the breeder is concerned with characters hardly, if at all, recognizable by eye. A considerable list of such could be cited in which the quality of the various grains used in the preparation of foodstuffs would take a prominent place. The quality of various fibres obtained from such crops as cotton, jute and flax, or of the oils used for food purposes, soap making or in the manufacture of paints come into the same category. For information on these special features the plant breeder has almost invariably to look to the manufacturers who handle the crop in which he is interested. Then he has frequently to devise ways and

means for their detection and measurement on a few plants, for the growing on of sufficient bulks for factory trials is commonly physically impossible. Such tasks are often peculiarly difficult. Yet it will be admitted, after reading this book, that unexpectedly good progress has already been made with many important crops.

But the breeder's efforts are not concerned merely with problems of quality. In many cases he is now facing the task of synthesizing new breeds capable of cultivation in localities where some such climatic condition as the lack of an adequate rainfall or the shortness of the growing period inhibits their growth, with such success that it seems as if the fitting of plants into new environments will soon be a commonplace matter.

Of even greater importance are the attempts now being made to mitigate the losses caused by fungoid and insect pests. A considerable body of evidence has now been accumulated, mainly by those engaged in economic plant breeding, that, even, if it is not often known what susceptibility and immunity to attack are actually due to, these features are nevertheless heritable. Thus in section after section of this book it will be found that breeding for disease resistance is part and parcel of the investigator's work. This is notably the case with such crops as cotton and wheat. What the successful solution of these problems means, not only to the cultivator who runs the risks of seeing his crops wiped out, but to all concerned with them, can only be imagined. But it is now clear that only continuous effort along clearly defined lines is required for obtaining a far greater measure of control over plant diseases than was ever dreamed of before Mendel's work set the course for the modern plant breeder.

The value of this book lies not only in showing concisely how, in a single generation, a surprising degree of control has been obtained over many of the important crop plants, but in the promise it holds out that the ingenuity of the plant breeder may yet solve many of the pressing problems which confront those whose business it is either to raise them or handle them commercially.

CAMBRIDGE. R. H. BIFFEN.

PREFACE

It might be inferred from the title of this book that its object was to present a complete record of all recent investigations with crop plants. Such, however, is the magnitude of modern work of this character that it is impossible to compass the most condensed account in a volume of this size. In the following pages we have accordingly attempted to present in a connected form the results of only such investigations as have advanced beyond the limits of purely academic interest and the outcome of which has been the introduction of improved varieties into general agricultural use. Even adopting this restricted basis, it has been found impossible to include everything that is desired, but it is hoped that the accounts that appear will furnish ample illustrations of the general direction of progress, whilst they may also serve to indicate some of the many new problems that have emerged and await solution before further advance is made possible.

We have utilized the published accounts of various investigations very fully, and would now avail ourselves of the opportunity of acknowledging our indebtedness to the many authors whose publications have been consulted.

We are also indebted to the Assistant Director and the Staff of the Imperial Bureau of Plant Genetics, and to Mr. F. A. Buttress, the Assistant Librarian of the School of Agriculture, Cambridge, for their ready assistance at all times, which has very greatly facilitated reference to a wide range of publications.

H. H.

H. M. L.

Cambridge.

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ERRATA

Page 229, line 7, *for* Kellaney *read* Kelaney.
,, ,, ,, 36, *for* Sengsbusch *read* Sengbusch.

RECENT ADVANCES IN AGRICULTURAL PLANT BREEDING

INTRODUCTION

It is impossible to state with any definiteness when and under what circumstances man began to exercise selective control over the plants he cultivated. That at the outset he must have been stimulated in the choice of material by some properties peculiarly adapted to his requirements is undeniable, but records of the course of progress from the initial choice until the time at which he grew his plants intensively are denied us. With the progress of archæological research, however, we are gradually extending our knowledge of the characters of many of the early cultivated plants, but apparently the manner of cultivation must still remain largely a matter of speculation. In much later times Greek and Roman writers showed by their repeated admonitions on what they considered should constitute the character of agricultural seeds, and on the manner of selection, that they realized the necessity of some form of selection to maintain the standard they had reached ; at the same time they appeared to be ignorant of the principles underlying permanent improvement.

Although there is evidence of a gradual and almost universal adoption of some form of selection in mediæval times, no marked progress was evident until the early years of the nineteenth century when some more than usually discerning improvers of self-fertilizing crops fell unconsciously on the value of single plants exhibiting outstanding merits. Individual investigators, indeed, proceeded a step further and adopted an elaborate system of continued selection within the produce of single plants, but it is still debatable whether changes can be brought about in normally self-fertilizing plants by these means.

The choice of individuals for propagation when based on well-defined morphological differences was an obvious line of procedure, but the relatively small number of such outstanding forms imposes a definite limit on the utility of this method of improvement. Thus, in the course of time selection was extended beyond forms of different morphology to forms of differing physiological attributes which, although less obvious in character, are potentially capable of contributing to both the final yield and quality of a crop.

In all these cases, however, the selectionist was operating on natural variations which could not be multiplied at will, and the possibility of further progress ceased with the complete exploration of available material.

Concurrently with this process of pure selection there was a gradual extension of attempts to secure new plants by hybridization, and the basis of selection was thereby broadened in a very significant manner. Unfortunately the products of hybridization in many cases exhibited a marked instability which no then-known method of selection appeared to be capable of eliminating, and this was the general position until Mendel's paper on "Experiments in Plant-Hybridisation," 1865, was re-published in 1901. It is no detraction of subsequent exponents of Mendel's conceptions to say that for clarity of exposition no one has exceeded that investigator himself.

The necessities of the position as Mendel conceived them may most appropriately be stated in his own words:

"Those who survey the work done in this department will arrive at the conviction that among all the numerous experiments made, not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which the offspring of hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations."

The view that Mendel propounded as the result of his experiments of the organization of the plant as a collection of separate unit characters that were capable of separate inheritance, placed the whole question of plant improvement on a new basis.

For the first time the plant breeder was offered an opportunity of producing new plants better suited to the many and very varied requirements of agriculture and commerce in an orderly manner, and although by its very nature plant breeding in many of its phases partakes largely of the attributes of an art, the underlying principles are now more clearly defined on a scientific basis.

It is the object of this volume to portray some of the advances that have been made in improving crop plants, more especially those that have been made with the specific object of meeting obvious agricultural needs. To the layman some of these will come as a surprise, for in many cases they stand as isolated examples of considerable accomplishments. To the plant breeder on the other hand, whilst they offer encouragement to further efforts, they will at the same time prove an antidote to over-extravagant expectations, for they expose the limitations which accompany all scientific investigations. As an indication of the latter the two important attributes of yield and quality may be instanced; in both these cases our knowledge is still most imperfect, and so long as it remains in this condition, the initial selection of parent plants for propagation must remain empirical, and depend in the early and really crucial stages on eye judgment.

The present-day plant breeder need not now suffer from the same degree of hybrid instability as troubled his fore-runners, but the many and varied plant-breeding efforts of the past thirty years have not yet enabled him to arrive at a system of selection that ensures fixity of the whole of the factors involved in any one character. Thus, although as a standard desirable of achievement he has been furnished with the conception of the pure line, that is, an unequivocably homozygous unit, in practice such a unit is extremely difficult to arrive at, and very few plants can be regarded as completely stable in respect of all characters. Indeed, the indications adduced from practice are that stability is a relative term, but that some varieties are more stable than others.

It may be advisable to state here that in order to view our subject in a right perspective plant improvement is not an absolute but rather a relative aim, conditioned first, and in some cases entirely by agricultural requirements, and secondly, by commercial

demands, and it is quite possible to conceive of an improvement of to-day proving an undesirability of to-morrow.

Queen Wilhelmina wheat, for instance, was undoubtedly a distinct improvement on the generality of soft wheats in use when it appeared. Nevertheless, although it still occupies an important position amongst present-day varieties, that position is a very specialized one, and the swing of demand has passed completely to varieties of wheat of a very different milling and baking quality.

Again, an improvement must be viewed in relation to the environment, that is, the soil and climatic conditions under which it is intended it should be grown. The old " land " varieties of cereals furnish an exceptionally apposite illustration of this qualification. Possessing, as they do in a remarkably high degree, hardiness and adaptability to soils of inferior fertility, the " land " varieties exhibit a distinct superiority to newer forms under conditions which demand these attributes, but are relatively very inferior under conditions more suitable to the newer forms. It is, of course, possible by mere selection to effect improvements amongst " land " varieties, for they are in reality populations of distinct ecotypes, but the utility of such selections is unlikely to extend far beyond the environmental range of the original population.

In very many instances, as the reader will observe, the desired improvements in the case of any one crop are determined to a large extent by commercial requirements. To appreciate the complete orientation of the breeder's problems it has thus been necessary to outline the principal features of various commercial processes in so far as they may have a bearing on the direction of breeding operations. Here again, however, it will be found that there is no absolute condition, but that requirements may differ not only from country to country, but in each country itself.

Whilst it may be true that the potential yields of varieties peculiar to definite geographical regions are superior to those of other equally definite regions, the returns actually realized are frequently determined by physiological attributes of the plant, such as resistance to drought, low temperatures, disease and insect attack. The hopes of improvement in many cases lie in the

discovery of forms exhibiting resistance in these directions, and at this particular juncture the operations of the plant physiologist, the mycologist, entomologist and plant breeder converge.

The many instances supplied in the following text illustrate the extent to which further advance is becoming increasingly dependant on the correct application of the results of investigations outside the range of what may be regarded as pure plant breeding.

In the main, plant breeding efforts during the past twenty-five years have been concerned with material produced by hybridizing varieties within separate species. Gradually, however, as information accruing from such studies has accumulated, it has become evident that, to secure the highest degree of some characters, more particularly disease resistance, species also must be brought under similar treatment. Finally, the range of cultivated plants available for man's use may be extended still further by the production of entirely new and hitherto unknown plants.

The lines on which the breeding of tropical crops has proceeded follow, in the main, the same principles, for these are fundamental, and, of necessity, apply to plants in general. But there are differences which may be briefly pointed out. Broadly speaking, tropical agriculture had not received the intensive empirical study which had been applied to the temperate crops before the novel ideas which originated with Mendel were brought to bear on the problems they presented. The tropical crops, as a group, bore a closer resemblance to the wild types ; were, in fact, less domesticated. A particular crop presented an admixture of varietal types. Sometimes, it is true, they exhibited a dominance of one particular type which amounted almost to a condition of purity, but evidence, if inconclusive, at least suggestive, points to the conclusion that such approximation to purity had arisen by the suppression, approaching elimination, of other types by natural, and not man's, agency. The type best adapted to the conditions survived ; but where, as was more often the case, the adaptation of more than one type was sufficiently close, a mixture of types formed the crop. Into this relatively primitive condition the breeder has stepped with all the latest teachings of science at his

command. The empirical work of the earlier investigators proceeds *pari passu* with the more advanced work of the modern plant breeder, and, not infrequently nor unnaturally, the older method is the quicker to yield practical results.

The second point of difference is the combination produced by a young country and a tropical climate. Vast areas of the tropics are only now coming under cultivation; crops are replacing a natural growth but the cropped areas remain islands in a sea in which nature's rule of the survival of the fittest still dominates. The condition of equilibrium established by nature is upset, but a new condition of equilibrium has not been established. That is true not merely of the tropics but of all young countries, such as Canada, which have only recently been subjected to the plough. But, superimposed on this, there is, in the tropics, a climatic factor which tends to stimulate all vital processes. Consequently disease assumes an importance hardly realized, or realizable, by one whose only experience is of temperate conditions, and it is less subject to control since the surrounding sea of natural growth forms an insuperable barrier to any direct attack on the organism responsible for the disease. In a few cases, it is true, direct attack has been attempted; the Cotton Stainer (*Dysdercus*) has been partially controlled by the elimination of its alternative Malvaceous host plants in the surrounding wild, and biological control has secured many noteworthy successes. But such cases remain the exception and, in the absence of conditions for successful direct control, indirect means must be sought and the production of disease-resistant forms becomes the main line of crop defence. To the plant breeder engaged on tropical crops the evolution of disease-resistant types may take precedence of questions of capacity to yield and of quality of product. It was the case in South Africa, where the continued existence of cotton as a crop was dependent on the discovery of a Jassid-resistant form, and it is the case in all cane-growing countries where resistence to *Mosaic* is the primary essential of any commercial cane.

The third difference may be traced to the youth of tropical agriculture in as far as it is concerned with exchange, as opposed to maintenance cultures, which latter supply the subsistence of

the indigenous population. Temperate-climate agriculture has become specialized to the extent that certain branches, notably those concerned with permanent crops like fruits, are demarcated as special subjects. They no longer fall within the designation of agricultural crops. In tropical agriculture there is no such sharp demarcation. There is, it is true, a large number of fruits, the mango, the loquat, the litchi and so on, widely grown, but grown as a garden, or horticultural crop ; but there are other permanent crops, rubber, cacao, coffee, tea, which occupy an important place in tropical agriculture and definitely fall within the category of agricultural crops. If the fundamental objective of the breeder is, in these cases too, to determine the constitution of the plant in terms of unit characters, his practical objective is somewhat different. No longer is it possible to raise large numbers from controlled matings, for questions of space forbid this ; nor is it practicable to extract "pure" types, for the span of a single generation is too long. In these cases the conception of the "clone" plays a prominent part, a conception not associated with agricultural crops in temperate climates. Thus are brought within the orbit of the tropical plant breeder the problems with which the temperate fruit grower is familiar ; the problems of differential varietal fertility, of relation between stock and scion, and, since the individual members of the clone have each a dual constitution, of the stock as a bearer of particulate characters. The importance of the stock is only now gaining gradual recognition but it is hardly to be doubted that uniformity of stock has an importance less than uniformity in the scion. To secure the desired uniformity offers a problem to the tropical breeder which finds its counterpart, in temperate regions, in fruit culture and not in agriculture in the narrower and general acceptation of the term.

As will become evident from the discussions that follow, improvement in plants is relative to the environment, *i.e.*, soil fertility and climate, in which the plants are grown and is not an absolute condition. By way of example reference may be made to certain manuring experiments made with different cereal varieties by Nilsson-Ehle, H., all of which stand well under normal conditions of manuring, but some of which were definitely stronger

strawed than others. When 100 kg. per ha. of nitrate of soda were applied to these varieties the increase in yield was the same for all of them, but the further addition of the same quantity of fertilizer produced a markedly greater increase in the strong-strawed forms. Again, the highest increase in spring wheats was obtained only when the variety was sufficiently early ripening.

Finally, it was shown that the absolute increase in yield from a given quantity of manure is greater for high-yielding than for low-yielding types. Consequently the yield potentiality of some varieties can be determined under conditions of high farming only. Inversely from this it may be inferred that the relative yield of lower-yielding types is greater under normal or subnormal conditions.

The phenomena here indicated and illustrated by the case of cereals in Sweden, are not peculiar to agriculture in the temperate zone; many examples drawn from tropical and sub-tropical agriculture could be adduced. It will here be sufficient to illustrate the point by two examples drawn from the personal experience of one of the authors. The early Pusa wheats, the product of the work of the Howards at Pusa, India, marked a considerable improvement on the wheats commonly grown by the cultivator of northern India. They possessed a high yielding capacity which, had it been developed under the standard conditions of wheat cultivation, would have brought about the complete supercession of the local varieties. Actually the increased yield, though definite, was small, too small to receive general acceptance by the cultivator. Extensive though the area under these Pusa wheats became, it constituted but a small proportion of the total wheat area and fell far short of complete replacement. In certain areas, however, sugar-cane enters into the rotation which, with the high manurial requirement, necessitates a standard of agriculture above the normal. Here wheat following cane may give double, and more than double, the normal yield. Under these conditions the Pusa wheats with their stronger straw lead to a realization of these enhanced yields while the local wheats do not, since, with their weaker straw, they are unable to carry the load indicated by such yields.

The second example is drawn from the same area : the bulk of the cane grown in these parts was, until recently, of the *Ukh* group of varieties, thin canes which normally yielded some 10 to 12 tons only. In the agricultural development of cane cultivation, by heavy manuring, trenching and better regulated irrigation, yields up to 35 tons were obtained ; but it was found that the *Ukh* canes under these conditions failed to ripen and gave a very low sucrose content. The advantage of improved agricultural methods only developed into an economic reality when the standard *Ukh* canes were replaced, first by Noble canes, many of which were uncultivable under the standard system of agriculture, and later by canes of the Coimbatore series, many of which were able to develop yield and maturity under the higher standards.

These are merely two instances, if striking ones, which support the view, here expressed, that plant improvement is a relative term to be interpreted in terms of the environment. In the former case, that of wheat, it is a question merely of failure to develop the potentialities of the " improved " variety under standard conditions of cultivation. In the latter case, that of cane, the matter goes further : not only will many of the improved canes fail to produce a crop under the standard conditions but the unimproved cane will be equally unproductive of sugar under the higher standard of agriculture gradually being adopted. Were no agricultural improvement feasible, many of the newer canes could not be regarded in the light of improvements. So closely are the efforts of the plant breeder and of the agriculturist interlinked !

PART I

CROPS OF THE TEMPERATE REGIONS

CHAPTER I

WHEAT (*TRITICUM sp.*)

THE genus Triticum consists of three well-defined groups of species. The first group contains the wild grass *T. œgilopoides* and the species *T. monococcum*, or one-grained wheat, which is grown as a forage crop in isolated mountainous regions in Europe.

The second group contains seven species; one of these is *T. durum*, the macaroni wheat, and another, *T. dicoccum*, a species with a well-marked degree of resistance to certain parasitic fungi, but otherwise of very limited commercial value. A further species of this group is *T. turgidum*, of which Rivet and Cone are examples.

The third group contains four species of which *T. vulgare*, since it is the most extensively used for bread-making among civilized peoples to-day, is the most important of this and of the three groups. It is highly probable that Afghanistan was the original home of this species, but it has spread widely not only throughout Europe and Asia, but in the three other Continents also.

The three groups are differentiated cytologically by possessing 14, 28 and 42 chromosomes respectively. This is a feature of particular importance in inter-species crosses, for whereas hybrids obtained between the 28 and 42 chromosome groups are moderately fertile, those between the 14 and 42 groups are sterile or weakly fertile. The important bearing of these facts on breeding practice will become more obvious in later pages.

Advances in the organizations of civilized peoples have played a silent but irresistible part in bringing about fundamental changes

in the extent to which certain classes of wheats are cultivated. This has been effected by the slow, continually exerted pressure first of the miller and then of the baker. Concurrently social changes have brought about the centralization of much of the work of the household, formerly performed by individuals, in well organized concerns, capable of producing such foods as bread in large quantities. As a result, domestic bread-making is largely a lost art, and excepting in small isolated places, peoples of all nations are rapidly becoming entirely dependent upon baking organizations for their bread supply. Thus, whether the position arose out of a demand on the part of the public, or proceeded from an educated taste for a light, well-aerated bread, the effect has been to create a demand for wheats of a particular quality.

Apart from botanical differences, for the production of flour for bread-making, varieties of wheats belonging to the species *T. vulgare* are divided into what are termed " hard " and " soft " wheats. These terms do not necessarily bear any relation to the " condition " of the grain, *i.e.* to the amount of moisture it may contain, although in fact hard wheats produced in the British Isles generally contain less moisture than soft ones grown under the same conditions. The use of the term " hard " probably arose from the fact that grains of varieties of that class are characterized by a steely appearance when fractured, whilst the interior of soft wheats is more commonly white, starchy and mealy. " Hard " wheats are not uncommonly spoken of as " strong " and " soft " wheats as " weak."

To the advent and subsequent development of hard wheats many of the changes in wheat production, at least in Canada, the United States of America and the British Isles, are closely related. The relative values of hard and soft wheats for milling and baking depend on several features. First, hard wheats can be milled in such a way as to produce a larger percentage of flour, and, consequently, a smaller proportion of offals than soft wheats, for in the latter it is difficult to obtain a complete separation of the endosperm from the pericarp or skin of the grain. Secondly, the endosperm of hard wheats is more granular, and consequently more readily and perfectly reducible to a state of fine division, than that

of soft wheats, which in addition offers considerable resistance to sifting through the fine, silken screens of modern mills.

These are the main physical attributes, important doubtless in their bearing, but insufficient to account wholly for the high favour in which hard wheats are held. The full reason for this only becomes fully manifest in the bakehouse: here it is found that the flours obtained from hard wheat, which possess a larger quantity of highly resilient gluten, are capable of absorbing more water in the dough. They hold this additional quantity of water throughout the entire process of bread-making, and consequently produce more loaves per sack of flour than soft wheats—an important criterion of value to the baker. The dough of a strong flour has more "body," is tougher, and does not tend to flow during handling. Moreover, a strong flour produces a larger, better-risen and more attractive loaf because its gluten is able to hold the gas liberated during fermentation more completely (Fisher, 1931).

The extended cultivation of wheat displaying these valuable economic characteristics was thus a matter of considerable moment in the history of the crop. The most notable variety of this description is Red Fife, which, not only by reason of the large and important part it has played in the earlier development of Canada and large areas in the United States of America, but as one of the parents of many hybrid varieties developed more recently in all parts of the world, is a landmark in the improvement of the crop.

As the first half of its appellation implies, Red Fife is a red-grained wheat, the latter half of the name is that of a Scots farmer who settled in Ontario early in the nineteenth century. It is recorded that about 1842 Fife procured some wheat from a friend in Glasgow, who in his turn had obtained it from a cargo landed in that city direct from Danzig. Fife sowed this wheat, but it proved to be a winter sort, and with the exception of one all the plants failed to ripen. Fortunately, this one plant was saved and its produce carefully preserved and then re-sown for several seasons. (Buller, 1919.)

In the course of time Red Fife, as it soon became known, was widely distributed and ultimately (about 1880) replaced the softer wheats in use up to that time. Apart from its own valuable

characters, the extended cultivation was favourably influenced by changes in milling operations which were brought about between 1870 and 1880. These consisted in improvements which permitted of the more perfect separation of the finer particles of bran, thereby effecting a distinct improvement in the colour of the flour. The good milling and baking properties of hard wheats such as Fife were well known, so that once the disadvantage of colour, due to particles of red bran being left in the flour, was removed, they were placed on terms of effective competition with previously favoured soft wheats.

The immediate result was that hard, spring wheats rose rapidly in favour and demand on both sides of the Atlantic, the acreages devoted to them increased, bringing in its train a fall in prices of both hard and soft wheats, but more particularly of the latter. This brought about a most serious decrease in the acreage devoted to wheat in the British Isles. The introduction of Red Fife was, indeed, the stimulus to the many efforts that have been made in different parts of the world to produce new varieties possessing good milling and baking quality, combined with those features of other varieties which rendered them suited to the conditions under which they were customarily grown.

In Canada, the first transatlantic home of Red Fife, one outstanding feature of wheat cultivation is the short period of growth of spring varieties which, because of the severity of the winter, form the bulk of the wheats grown there. The most serious difficulties facing the Canadian wheat-grower are drought, early autumn frost, and attacks of Black Stem Rust (*Puccinia graminis*). On occasions, heavy hailstone storms prove disastrous, but as compared with other factors they are spasmodic, and usually strictly localized. Sowing is done in April and May as soon as the frost is out of the ground, and the soil is in a fit condition to receive the seed. The crop is fit to harvest between, approximately, the middle of August and September 20th. Thus, whereas the Continental and British wheat-grower, if he uses winter wheats, is accustomed to a period of growth of, say, 250 to 270 days, *i.e.*, November to July or August, with Canadian spring wheats there are only 90 to 100 days between sowing and harvesting. More-

over, an extension of the normal period of growth may bring the wheat crop within the range of early autumn frosts, which cause a cessation in the normal process of translocation of material from the straw, and the grain is then in consequence shrivelled. As frosted wheat will not keep well, and in any case mills indifferently, it is either rejected by buyers, or purchased by them at a much reduced rate. Consequently, the maintenance of the acreage in some districts is directly dependent on a certainty of a very definite length of growth period, whilst an extension in acreage in a northerly direction can only be realized by the production of wheats of a still shorter period of growth.

A reduction in the very serious risk of frosting was brought about by the introduction of Marquis wheat, which, when judged on the basis of its actual acreage, must be regarded as one of the most remunerative plant-breeding results yet obtained. Marquis wheat was obtained as a selection made from the progeny of a cross between an early-ripening Indian wheat known commercially as Hard Red Calcutta, and Red Fife. The cross was actually made in 1892, but it was not until 1904 that the particular selection, which was to become famous later under the name of Marquis, was made by Dr. C. E. Saunders, at that time Cerealist of the Dominion of Canada. After subjecting the selection to various tests, it was distributed to the public in 1909.

As Hard Red Calcutta is a recognized description of a mixture of wheats rather than of one variety, the characteristics of this parent of the new wheat must always be a matter of some speculation, excepting that its earliness in ripening is beyond question. Marquis in this particular respect occupies an intermediate position between its two parents : it ripens about a week earlier than Red Fife and by so doing, and, because it usually outyields and is at least of equal milling quality to that variety, it has largely replaced it.

In addition to the value attached to Marquis by reason of this character, it derives a further benefit by the manner in which earliness in ripening enables it to escape attacks of Black Stem Rust (*Puccinia graminis*). Marquis is not rust-resistant in the biological sense, but rust-escaping, since at the time of appear-

ance of the fungus the plant is so far advanced towards maturity that the effect of the disease is insignificant.

With the sharply defined limits of time prescribed by the passing of winter conditions on the one hand, and the advent of early autumn frosts on the other, the production of still earlier ripening hard wheats than Marquis offers a big field for the plant breeder. A guarantee of security against any form of damage to a crop that is beyond the farmer's control is an aspect of improvement that cannot be neglected.

Following the introduction of Marquis, Saunders produced Prelude and Ruby, two hard, spring wheats, the former being two weeks and the latter about 10 to 12 days earlier than Marquis. The yield of these three varieties varies inversely as their earliness. Thus, Marquis produces the heaviest yield and Prelude the smallest with Ruby occupying an intermediate position. This, however, is a general statement of an effect, and the relative value of varieties possessing different periods of growth will vary with the conditions under which they are grown. Consequently, whereas Marquis outyields Red Fife in places where the season is naturally short, so Prelude in similar circumstances would exhibit an advantage over Marquis. This is an example of a circumstance that should qualify every assessment of the effect of earliness on the actual, as distinct from the potential, productivity of varieties.

The parentage of each of the three wheats is as follows :—

Marquis:

Hard Red Calcutta × Red Fife
(Indian) (Galician, originally)

Marquis

(Earlier than Red Fife in short-season districts and under these conditions a heavier yielder.)

Ruby:

Gehun × Onega
(Himalayan) (Archangel)

Early Riga (very early, but poor yielder)

Downy Riga × Red Fife

Ruby

(Two and a half weeks earlier than Red Fife.)

Prelude:

Ladoga (Russian) × White Fife (believed to be a derivative of Red Fife)

Alpha × Hard Red Calcutta (Indian)

Fraser × Gehun (Himalayan)

Prelude

Garnet, another variety of somewhat the same character as Prelude and Ruby, was introduced in 1926. This wheat is the product of a cross between Preston A and Riga M, each in its turn being a selection from Preston and Early Riga, respectively. These again were hybrids obtained as follows :—

Ladoga (Russian) × Red Fife

Preston

Onega (Archangel) × Gehun (Himalayan)

Early Riga

Garnet is from five to sixteen days earlier than Marquis, but, as noted previously, the difference may be greater under conditions which tend to lateness in ripening. (Newman and Whiteside, 1927.)

The advent of wheats of such good milling and baking qualities as Red Fife brought about far-reaching changes in British agriculture. With the rapidly increasing acreage sown with that variety in Canada, huge quantities were available for export, and much of this surplus found its way to Britain at prices considerably lower than that at which the British farmer could produce his grain. The acreage in wheat in the British Isles contracted very rapidly in consequence, and, excepting during the abnormal period of the Great War, has continued to do so. Although a glut of high quality grain was an underlying reason for this result, there were several contributory causes, and one was that English varieties did not possess either the milling or baking qualities found in Red Fife; they were also in most years inferior in "condition" to imported wheat, and consequently, before they could be stored in

quantity and subsequently milled, they required to be dried artificially. This operation involved an addition to their original price by way of fuel, and on account of the loss of weight, of commonly as much as 7 to 10 per cent., and in wet seasons, considerably higher.

In a very important feature, however, British wheats exhibit a superiority—they usually produce much higher yields of grain and straw than foreign wheats; thus for the five years 1923—1927 the average yield of grain for Australia and the Argentine was $6\frac{3}{4}$ cwt. per acre, the United States $7\frac{3}{4}$ cwt., Canada $9\frac{1}{2}$ cwt.; in Europe during the same period France produced 11 cwt., Germany $14\frac{3}{4}$ cwt., and Holland 21 cwt. as compared with an average of $17\frac{1}{2}$ cwt. per acre in Great Britain and Northern Ireland.

An attempt to meet the new position was at length made (about 1900) by the Home Grown Wheat Committee of the National Association of British and Irish Millers, and one of their first experiments was an endeavour to ascertain whether Red Fife could be grown successfully in the British Isles. The answer they obtained was in the affirmative, but excepting in a few cases, which must be regarded as more or less exceptional, it did not crop satisfactorily, judged by British standards of cereal yields. But an important conclusion arising from these trials was that Red Fife retained its strength when grown under British conditions. More recently, as a consequence of the lapse of time, this conclusion has been amply verified by the following tests:

In 1922 the National Institute of Agricultural Botany at Cambridge (1924) grew a series of plots of Red Fife under their supervision at eleven centres in England and Wales. The seed used at all the centres was derived from a quantity of Red Fife obtained from the late Dr. W. Saunders of Ottawa, Canada, the successive produce of which had been grown in England for twenty-one seasons.

The object of these cultivations was to provide tabulum for milling and baking tests and relevant chemical analytical determinations, and from these it was hoped to arrive at a measure of the changes that might have occurred in the commercial value of Red Fife since its introduction into England. The season 1922

was unfavourable for the English wheat crop, but despite this circumstance the conclusion arrived at on this particular point, when judged by milling and baking tests, was that Red Fife had fully retained its distinguishing characters after twenty-one years' successive growth in England.

In 1929 a similar examination was made, but in this case a comparison was made with flour from No. 1 Northern Manitoba wheat grown in Canada in that year. The writers of the report on this comparison state " that crop No. 1 Northern Manitoba had a higher protein content than usual and was of very good quality according to current standards of excellence. Nevertheless, Red Fife grown at Cambridge in 1929 was substantially equal to it, which, of course, means that it was incomparably better in bread-making quality than ordinary English wheat. It means also that Red Fife did not suffer from the climatic conditions which affected prejudicially in 1929 the quality for bread-making purposes of all ordinary English varieties." It will be realized that the Red Fife crop of 1929 was the produce of twenty-eight years' successive growth in England (Humphries, Clover, and Humphries, 1931).

Following the earlier observations of the Committee, the next question that arose immediately was whether " strength " was a heritable character. At this stage the Committee secured the assistance of Professor Sir Rowland Biffen, Cambridge, to whose investigations on the manner of inheritance of the botanical, and, more particularly, the physiological characters of wheats the subsequent improvement of the crop is in a large measure due.

The varieties Biffen (1917) used in seeking a solution of this problem were Red Fife, and Rough Chaff—an old English variety now little grown, and although he was necessarily at that time unaware of the ability of Red Fife to maintain its quality unimpaired when grown under British conditions, his estimation of the potentiality of the variety in this respect has proved remarkably accurate. Rough Chaff was a typically weak variety with opaque, soft, floury grain, and in the bakehouse displayed the instability of dough associated with weak wheats ; it possessed, however, the usual high grain-yielding potentialities of English varieties.

The two varieties, one typically "hard" and the other equally typically "soft," were crossed, and the grains of the F_1 generation were all hard, there was no indication of a condition intermediate between the two parents. The F_2 generation of the cross exhibited segregation into strong and weak forms in the proportion, approximately, of three of the former to one of the latter. A series of selections was made from this generation, and multiplied until it was possible to carry out baking tests on the produce of the F_4 generation. These tests showed that the endosperm of the grain then was "either that of one parent or the other and that it was never a blend of both," and the baking trials confirmed the conclusion arrived at from the appearance of the grain.

Subsequently, a white-grained hard form was selected from the progeny of the cross, and when sufficient seed was available it was distributed for growing under ordinary farming conditions as Burgoyne's Fife. The grain produced from these trial lots maintained the standard of high quality exhibited by earlier cultivations, but the yield proved disappointing, for it usually fell below that of the very widely grown "soft" variety Squarehead's Master.

Notwithstanding its failure to meet the whole of the demands of the problem, Burgoyne's Fife demonstrated many of the possibilities of the synthetic construction of varieties, not the least of which was the production of a strong wheat with white grain—up to that time a combination generally considered to be impossible.

Whilst Burgoyne's Fife is now almost entirely a matter of academic interest only, two other wheats, named, respectively, Yeoman I and II, have come to be regarded as landmarks in wheat growing in the British Isles. They were both produced by Biffen from a cross of Red Fife and the English variety Browick, and the former was distributed for general cultivation in 1916. Both wheats are red-grained, and the grains possess in a high degree the physical attributes of the Red Fife parent, and of hard wheats generally. Where Burgoyne's Fife failed, however, Yeoman has succeeded, for field trials conducted over a series of years have demonstrated a yielding capacity superior to Squarehead's Master, and only slightly if at all inferior to Wilhelmina, which is

usually regarded as one of, if not the most prolific soft wheat in cultivation in Northern Europe.

In baking quality " the strength of the flour of Yeoman wheat is of about the same order as that of the grade known as London Households, or put in another way, the wheat is sufficiently strong to produce, when milled without any admixture, a flour from which a marketable loaf can be made." Again, " the loaves (of Yeoman) are in no way inferior to those consisting mainly of flour from imported wheat " (Biffen and Engledow, 1926).

Thus at last the gradual course of the deterioration of the baking quality of English wheats was arrested, but, fortunately, without in any way impairing their high grain-yielding capacity.

Yeoman II, which in most respects resembles Yeoman I closely, was selected from the heaviest yielding forms obtained from Browick × Red Fife on a total nitrogen basis. For purposes of comparison the best of these selections were tested in the bakehouse against English-grown Red Fife, and Canadian Manitoba Hard, where the former produced two-pound loaves of a volume of 3,475 c.c. and the latter of 3,275 c.c. The best of the hybrids under these conditions had a two-pound loaf volume of 3,325 c.c. The usual commercial loaf is produced from a mixture of hard and soft wheats and has a volume of about 3,000 c.c. Thus, the best Browick Fife derivative produced flour capable of giving a loaf capacity superior to that of flour of ordinary standards, and far in advance of that produced from soft English varieties. It will be observed that on this basis Yeoman II is slightly superior to Yeoman I.

Not the least remarkable feature of Yeoman is that, unlike the generality of hard wheats which are spring forms with a short period of growth, it is a winter variety under temperate climate conditions, with the concomitant attribute of a long period of growth and, like most such varieties, is relatively prolific.

Most readers are already familiar with the heavy toll exacted yearly by plant diseases. It will consequently be sufficient at this stage to draw attention to their universality in some form or another on the various crop plants. No country and no crop can claim immunity from their ravages, but as the existence of

varieties of crop plants exhibiting more or less definite degrees of resistance to specific diseases was previously known, the attempt to ascertain the manner of inheritance of resistance or susceptibility was a natural sequence to the exposition of Mendel's Law. Any attempt made in this direction would not be a new one, for the late Mr. William Farrer of New South Wales in pre-Mendelian days had bred a variety named Bobs, which possessed a considerable degree of resistance to Black Rust. But if the manner of inheritance and of immunity could be established, then the possibility of combining resistance to specific diseases with other desirable characters of economic value in one variety would resolve itself into a matter of pure experiment.

In some of Biffen's early investigations on disease resistance, he grouped a large number of varieties according to the intensity of attacks of Yellow Rust (*Puccinia glumarum*), the most serious form of *Puccinia* occurring in the British Isles, and was enabled thereby to arrive at forms displaying a high degree of susceptibility on the one hand, and of immunity on the other (1907–8). For his investigation of the manner of inheritance of this particular form of Rust he chose a single plant from a plot of Northern Duluth, which displayed immunity after twelve successive years' cultivation in England. This variety, known under the name of American Club, was crossed with Michigan Bronze, the most susceptible form he happened to find amongst those under observation. The F_1 plants in all cases proved very susceptible to Yellow Rust, nevertheless sufficient seed was obtained to raise over 2,000 plants in the F_2 generation, and these exhibited clear segregation into badly attacked and immune plants, which on counting were found to be present in the approximate ratio of three of the former class to one of the latter (1,609 to 523). Thus, the appearance of dominance of susceptibility to Yellow Rust in the F_1 plants was supported by the figures obtained in the F_2 generation, and both generations supplied ample proof of definite segregation. Having secured this information, Biffen immediately endeavoured to obtain a wheat possessing rust resistance combined with high grain yield, for which purpose he crossed a resistant Russian variety found in Ghurka, with Squarehead's Master, at that time the most widely

cultivated variety in England. From this cross a form was finally chosen which appeared to possess superior cropping power, an opinion which has since been amply corroborated by numerous yield trials. Little Joss, as the new wheat was named, does not possess the high milling and baking qualities of Red Fife and a great many of its derivatives, but is superior to that parent in yield, is resistant to Yellow Rust, and produces an abundance of long, clean, bright, good-standing straw. Little Joss also exhibits a high degree of adaptability to light soils, and in this respect alone is a notable addition to the list of British varieties.

Resistance to Rust is a valuable feature at all times, but confers an additional value on a variety when a crop is grown intensively, for the high fertility of the soil causes vigorous vegetative development, and the plant is then more than usually open to attacks of fungoid diseases.

As the preceding accounts show, the general direction of change in the character of varieties cultivated in America and Canada in the last quarter of a century has been towards the production of hard wheats. More recently it became increasingly evident in those countries that whilst it was eminently desirable to carry on a sustained effort to produce higher yielding varieties, the difference between yields of grain in years of heavy Rust infestation, and those in which that disease was less virulent, may be much greater than that normally existing between different varieties. In other words, Rust attack is a limiting factor in production, and consequently, before advantage can be taken of the higher grain yielding potentiality of new varieties, those varieties must be adequately secured against this virulent disease.

Plant breeding effort in Canada and the United States has thus become focussed upon the production of varieties of greater productivity and good milling and baking quality, combined with resistance to fungoid diseases, especially Rust.

As the United States and Canada are exporting countries, the question of the character of the world demand for wheat must influence the character of the grain they decide to produce. For reasons that have been discussed already, hard wheats are preferred for milling and baking, but it would be erroneous to infer therefrom

that soft wheats must be relegated to a position of complete uselessness. An outstanding feature of soft wheats such as are grown in north-western Europe is their high grain-yielding capacity. The winter types of this class readily outyield Red Fife and Marquis, and although the best of them is barely superior to Yeoman, the latter is essentially a wheat for soil in a high state of fertility. Incidentally it may be remarked that not the least remarkable feature of Yeoman is that, unlike most, if not all, the hard wheats which are spring forms with a short period of growth, it is a winter variety under temperate conditions with the concomitant attribute of a long period of growth and, like all such varieties, is relatively prolific.

No hard wheat has been obtained yet that is equal to Squarehead's Master on soils in a medium condition of fertility. Consequently, on such soils soft wheats will continue to be grown unless a sufficiently enhanced price is paid for hard wheats to compensate for any deficiency in yield. Soft wheats must be judged on the extent to which they can be utilized in the countries in which they are produced, and in conjunction with other factors which, although relatively small individually, in their total effect determine the economic position of varieties.

In the British Isles, for instance, large-berried wheats, a description applicable to most of the soft wheats in use, meet an increasing demand for poultry feeding. There is also a demand for varieties suitable for the production of biscuit-flour; in this category Wilhelmina wheat occupies a leading position. Again, wheat straw which is produced in the greatest abundance by soft wheat is a requisite of livestock farms.

In Western Europe, during the period under review, efforts have been directed mainly towards the production of higher yielding varieties, with those already in use as the basis of operations. This has been achieved in some measure by careful selection of many outstanding forms, but gradually this means of improvement has been supplemented by hybridization, which enables the plant breeder to obtain a recombination of one or more of a series of desirable features of one parent with, possibly, only one or a whole series of equally desirable characters of the other parent. By

hybridization it may be possible to secure high grain-yielding potentiality as such; it may also be the means of adding to the already ascertained high grain-yielding potentiality of a variety an enhanced degree of a physiological character which when present enables the variety to be cultivated under soil and climatic conditions which were formerly inimical to its growth. Thus, intensified degrees of winter hardiness furnish the means of cultivating certain high-yielding varieties in areas where formerly their cultivation was accompanied with undesirable uncertainty; earliness in ripening when intensified in some varieties has enabled such desirable forms to be grown in districts where formerly their lateness in ripening rendered their use in some areas inadvisable. Finally, amongst a number of characters of what may be regarded as of secondary importance, there is strength of straw—a feature that under the promotion of more intensive production is becoming increasingly important. Examples of such phases of improvement will be presented in detail when considering the work done in Sweden. It will also be observed that in that country, as in the British Isles, higher yield alone is insufficient to meet all present-day demands, and efforts have been, and are now being, made to combine superior milling and baking quality with the high grain yield of the best of the improved forms. Although the directions of change in America and Western Europe have been weighted in two directions, the one towards higher quality and the other towards higher yield, both are gradually converging; in America, high quality having been secured, efforts are now being directed towards obtaining higher yield, whilst in Europe, having obtained higher yields, attempts are being made to obtain improved quality. Fortunately, as Biffen's work shows, there is not necessarily anything antagonistic between the two attributes.

America

As might be expected from the fact that wheat is not an indigenous American genus, the development of the wheat crop in that continent depended for a long time on the introduction of foreign varieties. Among the many that were introduced from time to time there were some which proved well suited to their

new environment; others were just as unsuitable and were quickly eliminated from cultivation.

Notable examples of successful introductions are Turkey and Kharkof, hard, red, winter wheats; Baart and Federation, white, spring wheats; Arnautka and Kubanka, Durums; and Red Fife, a hard, red spring variety.

Many, if not all, of the introduced "varieties" were probably populations composed of numerous variants. In the process of time these populations were subjected to selection on the single plant or single ear basis, and many valuable varieties have been obtained in this manner and introduced into commerce. Such, for instance, are Kanred and Trumbull, Red Rock, Kota and Mindum. Kanred is a single ear selection made in 1906, by Dr. F. K. Roberts of the Kansas Agricultural Station, from a Crimean variety. It is slightly more winter hardy than Turkey, one of the most widely and extensively cultivated winter varieties in the United States, and possesses the additional value of being slightly earlier than that variety; it also exhibits some resistance to certain forms of Leaf and Stem Rust. In point of quality it nearly approximates Turkey.

Trumbull is a single plant selection from Fultz; Red Rock is a winter variety similar to Mediterranean; Kota is a wheat developed at the North Dakota Agricultural College, it is resistant to Rusts, and has consequently been used as a parent in the production of new Rust-resistant varieties. Mindum is a Durum variety which was distributed by the University Farm, St. Paul, Minnesota in 1907.

Of hybrids, the most important agriculturally and commercially is Marquis, the history of which has been given in detail already. Since its introduction into the United States between 1913 and 1914, Marquis has spread so rapidly that in 1919 no less than twelve million acres were devoted to it. During this time it has maintained the high quality noted in earlier years, and is now regarded as the standard in this respect in the United States.

Another important variety is Fulcaster, a soft, red wheat which was obtained as a hybrid between Fultz and Lancaster in 1886. Minturki, a very winter-hardy variety, was produced at the

Minnesota Agricultural Experiment Station, St. Paul, in 1902 by crossing Odessa and Turkey ; it is a red, semi-hard variety and was put into general use in 1919. Ruby and Garnet, the development of which has already been described, may also be included here.

The outstanding problem facing plant breeders in the spring wheat areas of the United States and Canada is that of producing varieties resistant, or, if possible, immune from Black Stem Rust (*Puccinia graminis tritici*) and Leaf Rust. The importance of the problem may be gauged from the fact that the area under spring varieties in Canada is approximately twenty-five million acres and in the United States it exceeds twenty million acres, all of which is sown mainly with Blue Stem and Fife derivatives, none of which is resistant to the attacks of this parasite.

The introduction and distribution of Arnautka about 1900, and of Kubanka at about the same time, both varieties of *T. durum* and both exhibiting marked resistance to Stem Rust, marks an attempt to cope with this serious trouble. But these and all varieties of the *durum* group lack the bread-making qualities of such *vulgare* types as Fife and Marquis, and although their introduction was succeeded by a rapid increase in the acreage devoted to them, especially in the northern wheat-growing areas, their commercial utilization is limited almost entirely to the production of semolina and macaroni.

At one time it was thought that Marquis, although not genetically resistant to Rust, might, because of its earliness, escape serious damage, but it does so to an extremely limited extent only.

A severe epidemic of Rust in 1916 brought three resistant *durum* wheats, Acme, Monad and Pentad, into prominence. Acme is a single plant selection made from Kubanka and, in addition to being very resistant to Rust, is a high-yielding variety. Monad was introduced from Russia by Professor Bolley of the North Dakota Agricultural Experiment Station ; it is as resistant as Acme, but its grain is of somewhat better milling quality. Pentad, also introduced from Russia by Professor Bolley, is valued for its Rust resistance, but its milling and baking qualities are very inferior.

In 1919, Kota, another variety obtained in Russia by Professor Bolley, was distributed. This wheat is resistant to many forms of Stem Rust and is drought-resistant; it also possesses good milling and bread-making qualities (Waldron and Clark, 1919).

The value of a variety can never be determined entirely by its ability to resist attacks of parasitic fungi, and to-day, in the face of keen competition, other physiological characters such as yield, milling and baking qualities, and winter-hardiness demand attention. Although the varieties just mentioned possess varying degrees of resistance to Rust, only Kota can be claimed to produce grain of sufficiently good quality to comply with existing demands.

The problem of obtaining resistant varieties was complicated from the outset by the fact, established by many investigators, of the failure of some varieties to maintain their resistance from year to year or from place to place, and the underlying reason of this was found ultimately to lie in the existence of physiological forms of Rust. These specialized forms differ in their nature with the locality and their prevalence is subject to yearly variation. Since the existence of physiological forms was established by Stakman and Piemeisel in 1917, they have been subjected to systematic study and identification, and at least fifty forms have been recognized.

A striking example of the practical effect of this discovery is supplied by Stakman (1928): Kanred was distributed as a winter-hardy red, hard wheat and resistant to Stem Rust. Whilst resistant to about a dozen strains of Stem Rust it is, however, fully susceptible to others. Consequently, although very resistant in some seasons, it is just as severely attacked in others, and for this reason the cultivation of Kanred cannot be attended with any degree of confidence, and this variety is rapidly falling into disfavour amongst farmers.

The results of studies of the manner of inheritance of various physiological forms of Rust is the subject of a voluminous literature. It has been ascertained that in many cases single genetic factors control the resistance of definite series of biologic forms, but the factor controlling resistance to some forms in certain cases carries with it susceptibility to others. In addition, it has been shown

by Craigie (1931) that hybridization may take place in the æcidial stage, thereby giving rise to new forms of Rust differing from either parent and from any known existing form.

Finally, it has been found that the mature plant resistance is entirely independent of seedling resistance, and that this applies equally to all known forms of Rust.

It has long been recognized that whereas individual varieties of *vulgare*, which is a species of the 42 chromosome group, exhibit varying degrees of resistance to parasitic fungi, certain species of the group with 14–28 chromosomes are distinguished by marked resistance, amounting in some cases to almost complete immunity from these diseases. Evidence of the appreciation of this fact in practice is supplied by the introduction and rapid spread of varieties of *T. durum* in the United States, notably in North and South Dakota. It has been stated also by an American authority that "no Rust form yet encountered readily attacks Emmer in the field, where it has been grown for nearly fifty years" (J. A. Clark, 1928).

In North and South Dakota, *durum* varieties out-yield many of the *vulgare* types, but although they appear hard the flour produced from them is unsuitable for ordinary breadmaking, in addition to which it is yellowish in colour. The *durums* consequently, as already mentioned, are mainly utilized in the manufacture of semolina and macaroni, whilst the Emmers are used almost entirely for stock-feeding.

Most significant developments have occurred since 1920. Hayes, Parker and Kurtzweil reported the practicability of obtaining the Rust resistance of *durum* in *vulgare* types: for the variety Iumillo was crossed with Marquis, and one of the hybrid forms obtained therefrom, and afterwards named Marquillo, was found to be highly Rust resistant. Marquillo is a true *vulgare* type with 42 chromosomes.

In 1916, McFadden crossed Yaroslav Emmer (*T. dicoccum*) and Marquis. The Emmers, like the *durums*, belong to the 28 chromosome group, but the two species nevertheless differ in several morphological characters. In *T. dicoccum* there are usually two florets to each spikelet, a number that is not very often exceeded.

The glumes are tough, and the particularly brittle rachis fractures just above each spikelet. The existence of tough glumes renders threshing a difficult operation, whilst the character of brittle rachis, which *T. dicoccum* possesses in common with other species of the 14 chromosome group, renders loss by shattering a frequent occurrence.

The quality of the grain of Emmer wheat is greatly inferior to that of most of the *vulgares*, but particularly of the varieties of that species which now furnish the standard of milling and baking quality.

The Yaroslav Emmer used as a parent by McFadden, however, possessed a high degree of resistance to Stem and Leaf Rust, and tough, flexible straw that was particularly resistant to damage by wind and hail.

The F_1 plant produced a large number of ears, but exhibited a great deal of sterility, and only 100 seeds were obtained from it. These gave an F_2 generation of about 100 plants, all so unpromising in appearance that the breeder decided to delay selection for a time, and to grow the produce of the whole as a population in 1919. This proved a bad Rust year, and provided the first opportunity of separating resistant and susceptible types.

From about 400 to 500 plants grown in 1920 (F_4), 100 were tentatively selected, but with the exception of six they were all discarded. The six retained exhibited *vulgare* characteristics and *were free, or nearly so, from all recognizable diseases.*

The six selections were increased in quantity in 1921, in which year they were again free from Stem Rust and only slightly attacked by Leaf Rust, and it is noteworthy that both Marquis and Kota, which were used as checks in this season, developed Rust. After a re-selection, made on the basis of kernel type, the various lots were further developed in 1922. In that year there was a severe hailstorm about harvest which completely destroyed the checks and many of the selections, but fortunately left uninjured certain forms which had inherited the strong chaff and resilient straw of the Emmer parent. The remnants from this unforeseen but fortunate test were again re-selected and sown in 1923, when a quite unusually severe visitation of Stem Rust fur-

nished a further valuable test, for while the selections remained entirely free from the disease, the check variety, Marquis, showed 100 per cent. infection.

McFadden was also able to show that there was no linkage between any of the desirable Emmer characteristics and any other characters. Hence the possibility of obtaining high resistance to all physiological forms of Rust combined with desirable agronomic and commercial characteristics was demonstrated.

The most promising of McFadden's selections of the cross was named Hope, and another selection is denominated H–44–24.

It is noteworthy also that selections of the Marquis × Emmer cross exhibited a high degree of resistance to Smut and Bunt.

A further example of the production of inter-species crosses is provided by a cross made between Marquis and a *durum* wheat known as Pentad, which is highly Rust resistant. From this cross a form has been obtained which, whilst possessing the Pentad type of resistance, is a beardless *vulgare* wheat.

In all the three inter-species crosses mentioned above the numerical ratios of forms obtained on segregation were complicated, as is invariably the case with hybrids obtained from parents with different chromosome numbers, but this does not necessarily offer an insuperable obstacle to the production of new forms with *vulgare* characteristics possessing the high disease resistance of *durum* and Emmer.

In addition to the very considerable value these products of inter-species crosses themselves possess, they may be regarded as providing a new starting point for the production of what may be a valuable series of new forms. Thus, Goulden and Neatby (1931) have shown already that the yields of such standard varieties as Marquis, Garnet and Reward are inferior to those of certain hybrid selections from H–44–24 × Marquis, and Pentad × Marquis, on the average of trials in the three years 1928, 1929 and 1930, in the former two of which there was very little Rust, but in 1930 there was a severe epidemic. The figures indicate, as might be expected, that the superiority of the strains was most evident in 1930, when Stem Rust was epidemic.

Goulden and Neatby further state (p. 860 *loc. cit.*): "The results obtained to date indicate that the mature plant resistance of H-44-24 and Hope is equally effective, or nearly so, with all known physiological forms. If this is actually the case, all physiological forms may be regarded as one from a breeding standpoint."

Finally, the baking tests indicate that the quality of many of the strains obtained from H-44-24 × Marquis and Pentad × Marquis is fully equal to that of Marquis itself.

Goulden and Neatby draw attention to a possible difficulty in connection with the mature plant resistance, namely, its association with undesirable characters, since it was found in H-44-24 × Marquis that the Rust resistance of H-44-24 was linked closely with susceptibility to Black Chaff. They express the opinion, however, that although the linkage is genetic, it may be broken by growing sufficiently large hybrid populations.

Again, weakness of straw may be associated with mature plant Rust resistance, but in this case association has been broken already and plants have been obtained with high Rust resistance and sufficiently strong straw.

Although Hope has been found so satisfactory in the United States from a resistance point of view, it may be noted that Abbott found both Khapli Emmer and Hope susceptible to *Puccinia graminis tritici* in Peru in 1928, 1929. He reports that Hope rusted more severely than Khapli, many pustules appearing on the culms, necks, leaf bases, glumes and awns. "Many culms broke when the kernels were still in the milk stage and the kernels from heads that matured were badly shrivelled." Abbott concludes from his observations that a new and virulent form of *Puccinia graminis tritici* exists in Peru.

Europe

On reviewing the position in Europe it is observed that Wilhelmina or Queen Wilhelmina has been and is still one of the most popular of the soft wheats; it is a prolific grain producer under what may be termed average soil conditions, and gives an abundant quantity of strong upstanding straw. In quality the

grain is inferior to Yeoman for breadmaking, but is valued highly for biscuit-making, and is also favoured as poultry food.

A particularly interesting account of the origin of Wilhelmina is furnished by Professor Broekema, who produced the variety. As the whole of this project was designed and carried out in pre-Mendelian days, the account of the reasons underlying each step in the formation of a new variety is unusually instructive. In the account given by its raiser it is shown that Wilhelmina was produced by crossing Squarehead's Master with Zeeuwsche, a variety grown extensively in Holland about 1890, and valued for its high grain-yielding potentiality, and the quality of its grain. Zeeuwsche, however, was not equal to Squarehead's Master in yield and it was ultimately largely displaced by that variety partly on this account, but also because the English variety possessed a stronger straw and was thereby better enabled to stand under conditions of high farming. On the other hand, the grain of Squarehead's Master was poor in quality and Broekema's object was to secure improvement in this direction without sacrificing any of the variety's obviously valuable characteristics.

The hybridized grains were sown in 1886, and with a clear idea of his objective Broekema selected the produce of five outstanding plants which he named Spijk I and II and Duivendaal IV, V and VI, all of which exhibited good grain quality associated with long but very stiff straw.

Not being fully assured that the produce he had then obtained was sufficiently like Squarehead's Master to secure for him the various features he was attempting to obtain, Broekema back-crossed two selected plants, one from Spijk I and the other from Duivendaal IV with Squarehead's Master. It was from Spijk I, or, as it may be written in full, Squarehead♀ × Zeeuwsche♂ × Squarehead♂, that Wilhelmina was obtained finally.

There has been a marked increase in the acreage devoted to wheat in Sweden since 1920, which has occurred concurrently with a decrease in the acreage of rye. This change, which affects winter wheats mostly, is attributable to several causes. First, the introduction of improved varieties of wheat has raised the average yield from 10 to between 15 and 16 sacks per acre, an increase

greatly in excess of corresponding improvements obtained with barley and oats. This relatively greater enhancement of productivity has placed wheat in a very favourable position with the farmer. Secondly, the straw of the improved varieties of wheat is superior in standing power to that of the usually cultivated ryes.

A fundamentally important feature of any new winter variety designed for use in Sweden is that it must be winter hardy. Previous to any systematic attempt at crop improvement in that country, there was in existence there a considerable number of indigenous winter varieties, all characterized by high, although perhaps varying, degrees of winter hardiness. It was ascertained, however, that in mild winters English Squarehead was superior in yield to these indigenous wheats by as much as 50 per cent. This very significant superiority stimulated plant breeders in Sweden to select the stock of English Squarehead they had procured, for, like most other stocks at that time, it consisted of a large number of distinct forms. They eventually decided on the extended propagation of four races which they named Extra Squarehead I, Extra Squarehead II, Grenadier and Pudel Vete, and these in one combination or another formed the basis of the scheme of further improvement.

After the selection of the superior lines of English Squarehead the Swedish investigators set themselves to produce hybrid varieties combining the high-yielding capacity and generally good straw of English Squarehead with the winter hardiness of indigenous sorts. Later, the original scheme was elaborated to comprehend an attempt to improve the milling and baking qualities of the most desirable of the new varieties, and thereby to render the country independent of supplies of hard wheat from external sources.

Concurrently there existed the necessity of providing varieties with good standing straw and possessing early ripening habits, for certain districts. The value of the former is obvious under any conditions, but is becoming more so with all cereals with the gradual advance in the fertility of cultivated land in the older countries where relatively intensive agriculture is practised.

There are, moreover, additional circumstances in operation : for instance, the production of varieties of high grain-yielding proclivities necessitates better standing straw to sustain the greater weight of grain ; the advent of cheaper artificial nitrogenous manures must result in the more liberal use of these fertilizers, particularly with wheat, and, finally, there is the position arising out of the combined use of high yielding varieties and nitrogenous fertilizers.

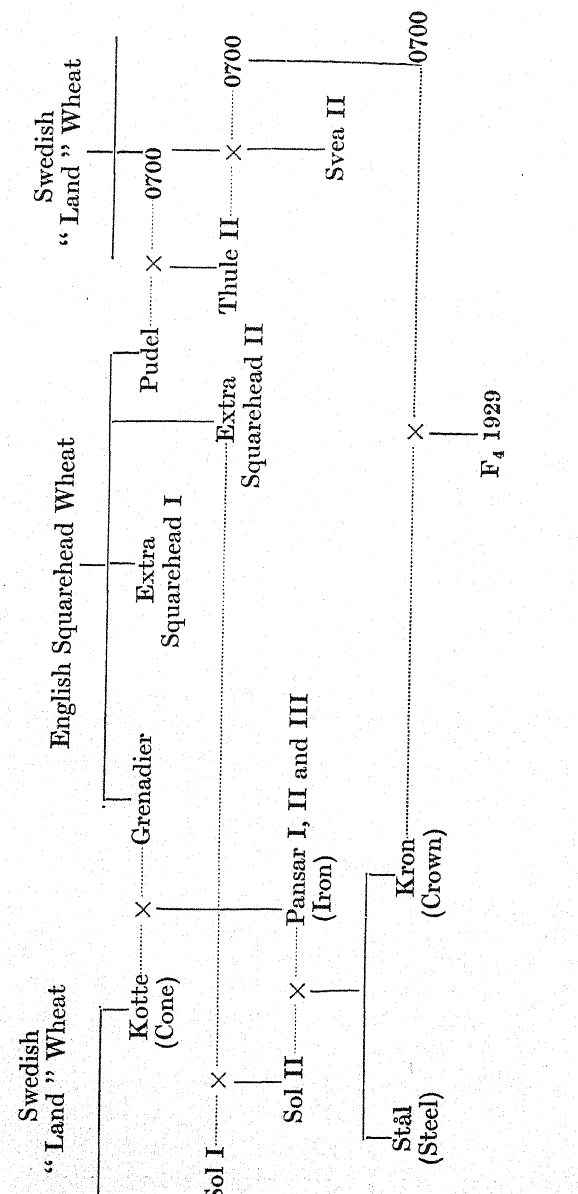
The problems just outlined necessitated a gradual building up of the desired varieties by steps, the rapidity of progress being determined largely by the success achieved in finding improved forms in the produce of each cross.

In 1905, Sammett wheat, an indigenous winter-hardy and early-ripening form from Central Sweden, was crossed with Pudel, a red-grained, relatively high-yielding selection with a good straw, obtained from English Squarehead. From this cross Thule I and II were obtained. These were both red-grained wheats, earlier ripening than Pudel, and characterized by good straw. Thule II was also more winter hardy than the parent Pudel, to which it was, however, approximately equal in yield. Thus, the new wheat was at once more valuable than the parent Pudel for the particular purpose in view.

Although possessing a higher degree of winter hardiness than Pudel, Thule II did not approximate closely enough in this respect to Sammett to be considered entirely satisfactory. It was accordingly back-crossed with Sammett, and the variety Svea II was produced, which was ascertained to be not only considerably hardier than Thule II but also possessed better baking qualities than that wheat.

Other examples of the production of improved varieties are provided by Pansar (Iron) and Sol II. Pansar was obtained by crossing the indigenous variety Kotte with Grenadier, one of the original selections from English Squarehead. Pansar is decidedly superior to Grenadier in yield and at the same time exhibits greater winter hardiness.

Sol II was produced by crossing Sol I, an indigenous variety characterized by good quality, winter hardiness and early ripen-


Swedish "Land" Wheat
Sol I
Kotte (Cone)
Sol II
Grenadier
Pansar I, II and III (Iron)
Stål (Steel)
Kron (Crown)
English Squarehead Wheat
Extra Squarehead I
Extra Squarehead II
Pudel
Swedish "Land" Wheat
0700
Thule II
0700
Svea II
0700
F_4 1929

ing, with Extra Squarehead II—another selection from English Squarehead.

A further step was the production of Kron and Stål (Steel) wheats from Pansar × Sol II. Both these wheats are high yielding and somewhat hardier than Pansar; Kron is, in addition, decidedly earlier than Pansar. Nevertheless, Kron is not as winter hardy as Sol II, and it has accordingly been back-crossed with that variety in the hope of securing a variety with the necessary degree of this character.

A general idea of the relative winter hardiness of some of the old wheats and of the new productions is supplied in the following Table:

10 = very hardy. 1 = very sensitive to frost.

10. Indigenous wheats from Central Sweden (0700, 0760, 0762, etc.)
9. Svea I and II, Jarl.
8. Bore II, Ankar.
7. Thule II, Sol III, Standard Wheat.
6. Stål, Kron, Pansar.
5. Extra-Squarehead II.
4. Smaa, Grenadier.
3. Wilhelmina.
2. English Squarehead.
1. Spring wheat from Halland and Dalarne.

As in other European countries, so in Sweden it has been found increasingly desirable in recent years to pay particular attention to the milling and baking qualities of the wheat produced there. The general character of high-quality varieties has already been commented upon. Apart from the higher milling and baking qualities of "hard" wheats, it is realized in Sweden, as elsewhere, that in years of abundance the relatively larger quantities of "weak" wheats available on the market tend to produce relatively low prices for them, consequently the production of varieties of high quality is desirable both for their own intrinsic high milling value, and as a means of ensuring a reasonable price for soft wheats.

From various baking tests conducted in Sweden it was ascer-

tained that Sammet was decidedly superior in baking capacity to any of the improved varieties, amongst which Thule II proved to be the best. Later, however, it was found that Svea II very nearly approximated to Sammet in this respect, and as its yielding capacity is higher and it has a better straw, it is a valuable variety, at least for Central Sweden. Svea, it will be recollected, originated from a back cross of Thule II with Sammet, and Thule II in its turn was obtained from Pudel (a selection from English Squarehead) crossed by Sammet. Svea thus furnishes an excellent illustration of the recombination of a series of characters from several parents.

Svea II is not sufficiently prolific for South Sweden, and for that province crosses between an early American winter wheat and Sol II and Pansar II have been made and their progenies are being investigated.

Spring Wheats. It may be rightly claimed that the introduction of high-yielding varieties furnished the original impetus towards the increased cultivation of spring wheats in Sweden, but legislative measures introduced by the Government of that country probably furnished an even stronger motive for the changes brought about in the acreage during the last few years.

In the period 1911–15 the acreage of spring wheat in Sweden was 7,067 hectars, whilst that of winter wheat was 108,648 hectars; in the same period the yield of spring wheat formed 4·2 per cent. of the total production. Since then the contribution of spring wheats to the total production has advanced to about 15 per cent., and the acreage at present is more than four times as great as it was in 1911–15.

Previous to the attempts to improve spring wheats, which will now be briefly related, there were several indigenous varieties in use and in addition a few imported sorts, amongst which was one of particular note, Heine's Kolben. This variety is regarded by the Swedish investigators as closely resembling Galician Kolben, a wheat grown formerly in Poland and East Germany. From Heine's Kolben a selection was made and named Svalöf's Kolben, and this was for many years the most successful spring variety in Sweden.

It is interesting to note that in many respects Kolben resembles Red Fife, and the similarity extends to the grain, which exhibits a high gluten content and produces flour of excellent baking quality. As the origin of Red Fife, as grown in Canada, has been traced to Galicia, it is probable that the two varieties originated from one source.

Kolben, in addition to exhibiting a higher-yielding capacity than indigenous varieties, was also stiffer strawed and more resistant to Yellow Rust (*Puccinia glumarum*).

One of the first crossings attempted was with a bearded wheat obtained from Emmer, a spring variety, and Svalöf's Kolben, from which Extra-Kolben I was raised. This new wheat proved superior in yield to both parents, but was approximately as early as the parent Svalöf's Kolben. Its one drawback was the straw, which was not so stiff as that of Svalöf's Kolben, but this was remedied in a selection made from Extra-Kolben I and named Extra-Kolben II.

Succeeding Kolben and Extra-Kolben, crosses were made with Schlanstedter, a prolific variety under favourable conditions, which is grown extensively on good land in Saxony. From both crosses varieties were obtained exhibiting higher yields than either Kolben, but they were characterized by a distinct tendency towards the requirement of special conditions to enable them to produce their maximum results, and the grain was not of particularly good quality.

In Sweden there are very sharply defined necessities for earliness as one progresses from the south to the north of the country. The indigenous spring wheats are about a week earlier than Kolben, and the cultivation of that variety is consequently restricted to coastal districts in South Sweden, and to certain warmer soils. But a series of new wheats obtained by crossing indigenous varieties with Kolben has produced desirable results; Rubin, for instance, was obtained from Dala × Kolben; it is decidedly earlier than the parent Kolben, but nevertheless gives an equally good yield and the straw is decidedly stiffer than Dala.

A cross between Halland and Kolben has produced a variety, Diamant, which marks the biggest advance in earliness associated

with high grain yield. Diamant is as early as Rubin and has even surpassed that variety in productivity. It also possesses a stiffer straw and more indication of high baking quality.

Breeding for Control of Insect Pests

The possibility of controlling insect pests of cereals by means of host resistance has recently come within the purview of the plant breeder, and although such studies are only in their infancy, there already appears to be legitimate reason to hope for advances in this direction.

In connection with the wheat crop, a report published in 1931 by Painter, Salmon and Parker gives an account of investigations made on the resistance of varieties of winter wheat to Hessian Fly (*Phytophaga destructor*), on occasions a pest of serious import in the United States. About 400 varieties were observed for fly infestation and the data obtained over a period of eight years enabled the investigators to group the varieties into (1) those which are highly resistant to fly from the hard wheat belt, (2) those with medium infestation, and (3) very susceptible strains.

For the purpose of a standard comparison all the counts of infestation, whether of plants or of tillers, were referred to one variety, Kanred, which, although exhibiting a high degree of susceptibility, was not the most susceptible variety that might have been chosen.

Of the fourteen varieties grouped as highly resistant the average per cent. of plants infested varied from 0 in Malakoff, Michigan Wonder, Red Rock and Schonacher, with corresponding controls of 62·1, 41·7, 44·8 and 33·3 in Kanred, to 3·0 in Beechwood with a control of 50·7. Of seventeen varieties grouped as heavily infested the highest per cent. infestation was in Turkey with 65·8 and control 42·6, and the lowest in Zimmerman, 30·5 with control 41·7.

A very important feature is commented on by the investigators which is "that varieties, selections and hybrid lines, whether homozygous or heterozygous for agronomic characters, may be mixed populations so far as type of reaction to Hessian Fly is concerned." This conclusion is substantiated by infestation

counts of a number of selections of the varieties Illini Chief and Fulcaster. The writers of the report draw attention to the fact that nearly all the varieties exhibiting marked resistance to the fly are soft wheats. Fulhard, the only hard wheat with low fly infestation, is a selection from Fulcaster, which is an old-established soft variety. Again, of the seventeen varieties showing heavy infestation there are only two soft wheats, Burbank and Zimmerman. One explanation offered for the circumstances is that soft wheats and Hessian Fly have been in association in the eastern United States for about 150 years, during which period natural selection may have operated in the direction of the survival of the more resistant types. On the other hand, the introduction of hard wheats in Kansas dates back for only about fifty-seven years, and the chances of the operation of natural selection have been correspondingly less.

A number of crosses of what have proved resistant and susceptible varieties was made, and the degree of infestation of the progenies studied. In a few cases tests were made on F_1 plants, and although the number of these employed was necessarily small, the results indicated a degree of infestation equal to that of the susceptible parent.

Similar studies of later generations indicated that some selections were as susceptible as the susceptible parent, others as resistant as the resistant parent, still others occupied an intermediate position. There was no indication that resistance was linked with any observed agronomic character.

The ultimate solution of the problem is complicated by several conditions which emerge from these studies. These are, (1) the decided difference in the number of flies which develop on the several varieties, (2) a tolerance of the fly by the host, whereby the pest develops without material damage to the host, (3) the ability of some varieties of wheat to develop fly better and faster than other varieties, (4) the ability to produce tillers after infestation, and (5) the stiffness of straw in relation to fly damage. The data presented refer to infestations from the hard-wheat belt in Kansas, but there is strong experimental and other evidence that there is a different strain of Hessian Fly prevalent in the soft-wheat area of

that State. Thus, whereas Illini Chief displayed a remarkable resistance to the fly from the hard wheat area as compared with Kanred, the data obtained from infestation of fly from the soft-wheat area show a higher average in Illini Chief than in Kanred, regardless of what criterion is used as a measure of infestation.

Wheat-Rye Hybrids

This account of the various developments in wheat breeding may be very fittingly concluded with notice of the production of the inter-generic plant, wheat-rye.

Several attempts to obtain hybrids of these two genera have been made during the last half century, but substantial progress has been long delayed owing to the high degree of sterility exhibited by all the progenies.

Recently, interest in the subject has been revived largely as a result of work carried out in Russia, since definite constant intermediate forms characterized by a high degree of fertility have been obtained there.

One of the earliest accounts of the hybrids obtained in Russia is given by Tjumjakoff (1927, 1930), working under the direction of Professor G. K. Meister and in conjunction with N. G. Meister, who describes how they were observed in 1918 as natural hybrids of winter wheat and rye where various lines of these two cereals were grown in contiguity. The wheat was always the female parent, and the hybrids all occurred in strain of *T. vulgare* var. *erythrospermum*. It was observed, however, that the hybrids appeared in very different numbers in different lines of this variety, in some they were found in considerable numbers, whilst in others they were extremely rare or entirely absent. The line in which an exceptionally large number of hybrid grains was obtained was one designated by the number 648.

These observations led to an attempt to produce similar hybrids on a larger scale, and for this purpose the best of the lines, *i.e.* those that had previously produced the largest numbers of hybrid grains, were sown in rows, and between every three or four of such rows one or two rows of winter rye were interspersed. A large number of hybrid grains was obtained in this manner; in 1923–24,

for instance, the progeny of line No. 648 produced 32 per cent. of hybrids. The gaining of this large percentage of hybrid grains in this and other lines resulted from the use of the poorly developed grains of the parent ears, whereas formerly sufficient care was not exercised in separating these thin, shrunken grains from the chaff on threshing.

In the period 1918–25, 18,150 hybrid plants were obtained, and from a total of 149,116 ears arising therefrom, 14,565 grains were produced. The fertility of the hybrids varied with climatic conditions, but those from each line of wheat exhibited a distinctly characteristic degree of fertility also. One plant is recorded to have produced 35 grains, but such a high degree of fertility was extremely rare. A large proportion of the grains of the F_1 plants failed to germinate, or produced plants that soon died. In all, about 5 per cent. of the grains that were sown produced plants that persisted.

In the F_2 generation, wheat-like, wheat-rye, intermediate, rye-wheat, and unquestionably rye-like types appeared. Tjumjakoff in a further account deals with certain features of the intermediate types: a numerical analysis of these in the F_2 showed that 43·4 per cent. were completely sterile, and those that were fertile exhibited a low fertility and usually segregated in F_3 into wheat and intermediate types, the latter segregating again in a similar fashion in succeeding generations.

A very large number of F_1 plants, namely 12,053, were obtained in 1924–25, which gave 11,197 grains, and from these 2,020 F_2 plants were raised. In this case certain of the intermediates exhibited an unusual degree of fertility. They were carried on into the F_3 and F_4 generations, but instead of segregating in the manner noted previously with other intermediate forms, they behaved as homozyogotes. Two of the constant intermediate forms were examined cytologically and found to have $2n = 56$ chromosomes, or the sum of the diploid number of the two parents (rye $2n = 14$; wheat (*vulgare*) $2n = 42$).

It appears from the figures given that the sterility which baffled earlier workers was still strongly in evidence, and although Tjumjakoff does not state the number of constant intermediate

forms obtained in the F_2, one gathers that it was only a very small proportion of the total number of plants of that generation. The necessity for working with large numbers to obtain the few possible fertile combinations is definitely emphasized. Nevertheless, it is evident from Tjumjakoff's observations (*loc. cit.*) that the degree of fertility is subject to a great deal of variation according to the parents used.

In the extent to which they are circumscribed by conditions to working with limited numbers, plant breeders may undoubtedly attribute much of the lack of success in inter-generic, and to a less extent in inter-species crosses.

Tjumjakoff's examination of the constant intermediate forms was continued in the F_3 and F_4 generations, but no segregation occurred, the plants maintaining an intermediate position and bearing a close approximation to the F_1 in respect of all characters observed. The percentage of normally developed pollen grains, however, which was lower in the F_2 than in the parents, increased in the F_3 and F_4 generations. In their modes of flowering the constant intermediate forms resembled wheat, for the stamens dehisced normally, and these two facts taken in conjunction imply a strong tendency to normal self-fertilization.

In F_3 both of the two families had a considerably lower percentage of normally developed pollen than the two parents, but in this generation there were also certain individuals with 100 per cent. good pollen.

Regarding the number of productive plants, there is a striking similarity in this respect in F_2, F_3 and F_4 generations. Both families showed 100 per cent. fertile normal ears and were characterized by high fertility in all plants, and in the whole of the ear.

The grain of the new cereal is typical of rye, and in absolute weight is intermediate between the two parents, but the lowest variant is less than rye and the highest variant is greater than wheat. In grain colour and in the shape of the embryo the hybrid resembles wheat.

There has not yet been sufficient opportunity to determine accurately the agricultural and commercial value of what in

reality is a new cereal. It is possible, nevertheless, to visualise its potential value, since with a combination of the physiological characters of rye and wheat it may be possible at one step to secure greater winter hardiness and an intensified adaptation to light soils in a cereal whose grain characters apparently approximates closely to wheat.

Some indication of the possibilities of the hybrid is furnished by Kharitonov (1930). Thus, in severe winters when the wheat parents almost perished and the rye parent was severely damaged, some of the hybrid forms proved definitely resistant to cold and drought. In three consecutive years, 76 per cent. were better than the wheat parent, 60 per cent. better than line 329, the most winter-resistant line of wheat, and 36 per cent. equal to rye.

Amongst the winter-resistant forms some are distinguished by high grain yields, others by an earliness in ripening equal to that of rye, others by grain of high quality, and others again respond differentially to variations in soil fertility. All but two hybrids out-yielded the standard by 20 to 60 per cent.

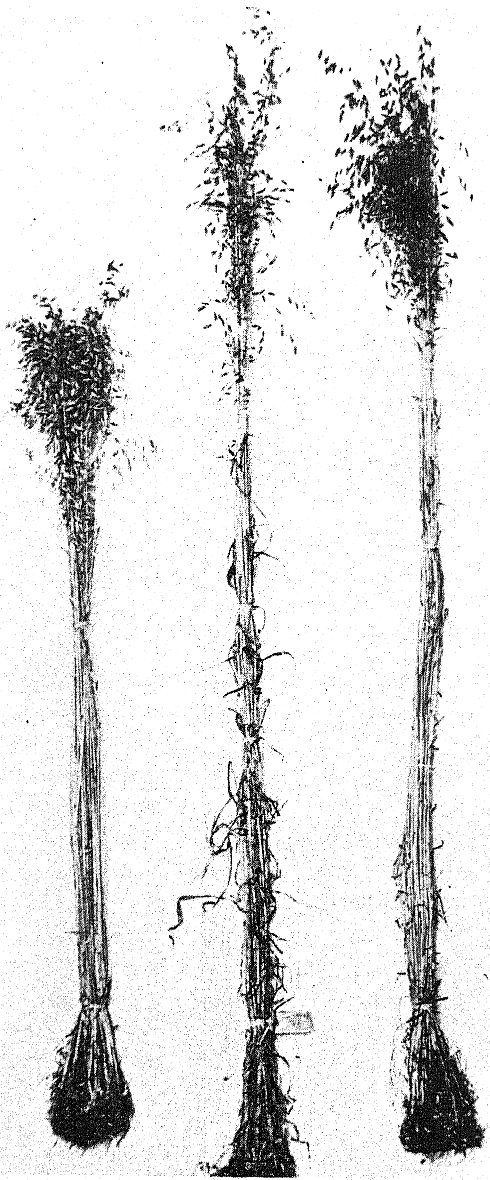
In certain preliminary baking tests one hybrid proved satisfactory, whilst others, judged by the appearance of the grain, are likely to reach at least as high a standard.

In the majority of cases the hybrids were superior to the standard wheat, line 329, in 1,000-corn weight, showed a higher proportion of vitreous grains, and certain families exhibited the combination of well-filled, heavy and vitreous grain.

Plant Breeding Procedure. As the actual breeding procedure adopted in the case of wheat, barley and oats is similar the stage now arrived at offers an opportunity of reviewing very briefly the procedure adopted in breeding practice, and of the interpretation of the results obtained, on a Mendelian basis.

In the main it has been found that, excepting in so far as they may be used as indications of associated quantitative and qualitative attributes, botanical characters provide very limited assistance in breeding. When the breeding objective is economic in character, the plant breeder finds himself concerned chiefly with physiological characters. These have been shown to be inherited in a like manner to botanical characters, although the exact ratios obtained

PLATE I



Fully grown and ripe plants of Argentine (*left*), Grey Winter (*right*). In the middle, specimen plants of a selection from the hybrid progeny of these two oats, exhibiting a positive transgressive segregation for length of straw.

[*To face* Plate II.

PLATE II

Fully grown and ripe plants of Argentine (*left*), Grey Winter (*right*). In the middle, specimen plants of a selection from the hybrid progeny of these two oats, exhibiting a negative transgressive segregation for length of straw.

[*To face p.* 44.

on segregation are more difficult to determine owing to the masking effect produced frequently by the environment.

The initial line of procedure adopted by plant breeders in all parts of the world has been to start with a variety which has been proved, by either the knowledge gained by long experience of that variety or by actual yield trials, to possess valuable economic characteristics. Almost invariably, however, even the best of such varieties exhibits limiting factors such as susceptibility to disease, lateness in ripening, poor standing straw and inferior grain quality. Amongst the many varieties in cultivation there are, fortunately, some that exhibit degrees of certain desirable characters far in excess of those found in what, because they exhibit the greater number of good features, may be denominated the basic varieties, and the object of hybridization is to obtain a combination of all these desirable features in one variety.

Whilst it is essential to retain in the hypothetical variety the good yield of the basic variety, yield of grain *per se* is probably the ultimate expression of many attributes. To proceed to ascertain the yield of the very large number of forms resulting from a single cross by actual quantitative tests is not practicable, and initial selection is necessarily determined largely by eye judgment. Despite these serious limitations, forms have been obtained which show a very close approximation to the parent that happens be superior in this respect, whilst other forms exhibit a decided to inferiority. There is consequently no reason to doubt the inheritance of yield on a Mendelian basis, although the proof of such a belief is extremely difficult to establish.

Nilsson-Ehle has shown that the colour of the grain of red wheat is probably due to a number of distinct, individual units which may operate separately, or may appear in different combinations and so furnish a graduated series from white to full red. The same may apply to physiological and other characters, and the number of combinations possible on hybridization is consequently an extremely large one, and the chance of the breeder alighting on a form exhibiting the same degree of a character as either parent in the hybrid progeny of two parents exhibiting different degrees of a character, is small. He may, however, pick

out one exhibiting a high degree of a particular character and by back crossing with the parent eventually arrive at a form exhibiting a near approach thereto. On the other hand, on occasions, a combination of a series of the various units occurs and transgressive segregation becomes evident, under which circumstances forms exhibiting a degree of a character in excess of that possessed by either parent are obtained. Such forms are manifestly extremely valuable not only in themselves, but also as a basis of further advance along the particular line in question. But, excepting under extremely fortunate circumstances, the production of new forms superior to those in existence is fundamentally a matter of the gradual addition of degrees of characters by a series of steps.

Many attempts have been made to analyse yield in cereals; it has been shown, for instance, that the tillering capacity, the number of grains per ear, and the weight per grain are fundamental expressions. But the conditions which induce one variety to tiller more abundantly than another, which determine in the first case the number of grains per ear, and then the weight of the individual grains, are extraordinarily complex even as separate expressions, and still more so in their ultimate effect on one another.

It is undoubted also that in many cases the enhanced value of a variety in respect of, say, yield, does not lie in a greater potential yield, but is attributable to some physiological cause, such as earliness in ripening, resistance to disease or specialized adaptability to definite soil conditions.

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CHAPTER II

BARLEY (*HORDEUM sp.*)

Barley is utilized for malting and as a food for livestock. For the latter purpose, since it contains more fibre than wheat, it is more easily consumed than that cereal, which tends to become pasty when fed alone, and makes swallowing difficult.

The quantity of feeding barley available on the world market is always largely in excess of that suitable for malting, and the price obtainable for the latter is consequently correspondingly higher, and this furnishes one reason why recent efforts to improve the barley crop have been concerned mainly with malting barley.

As the principal raw material in the manufacture of beer and to a large extent of whiskey, barley is valued primarily on the basis of the amount of starch it contains which can be readily converted into maltose, a fermentable polysaccharide.

Up to relatively recent times, malting barley was purchased almost entirely on its physical appearance. Good condition, that is, freedom from excessive moisture, is a primary qualification, for with too high an amount of moisture barley, like all cereal grain, is difficult to store safely in bulk for any length of time. Moreover, impaired germinating capacity is frequently a corollary of poor condition.

Apart from condition, full ripeness may be a criterion of quality, and is usually found concurrently with a distinctly finely reticulated palea or skin. Grain bearing these appearances when cut across exhibits a fine, white, mealy interior—one, that is, indeed, the direct opposite to that associated with good milling quality in wheat.

Beaven (1902) showed that the differences in the appearance in the interior of good and inferior samples of malting barley were related to the total nitrogen content of the grain, good malting barleys having a low, and inversely, poor malting barley a high

total nitrogen content. This finding has since been confirmed by many experimental results, and in normal malting practice.

If the total quantity of nitrogen is high it follows as a result that the quantity of carbohydrate, the largest constituent of the grain, will be correspondingly lower. Thus, the total quantity of nitrogen, or, more correctly, the total protein content, forms the principal basis of differentiation between barleys which come into the category of malting and those which are relegated to the feeding classes.

The difficulty experienced in obtaining a long life for beer owing to the presence of large quantities of readily fermentable protein in solution, and the longer time necessary to malt nitrogenous grain, are secondary factors.

The amount of protein in barley grain has been found to depend primarily on the variety, and on the nature of and the condition of fertility of the soil on which the crop is grown, and above all on the character of the season. Secondary contributory conditions are the time of sowing, the character of the seed, and the rate at which the seed is sown. These all affect the ultimate composition of the grain in a like manner, but not necessarily every variety to the same degree. Hence, included in this category there is finally the response of any particular variety to all the various possible combinations of the other conditions (Munro and Beaven, 1900).

It has been found that between the best and the least good malting varieties there are substantial differences in the total nitrogen content of the grain. But the largest differences found between varieties now in general use are much less than the seasonal difference existing in the case of any one variety (Hunter, 1926). To illustrate this point the figures given in the table on p. 51, taken from the Irish experimental plots, may be quoted; in these investigations the variety Archer served as a standard of comparison throughout.

It will be noted that the maximum difference, ·14, which, on a percentage basis, is equivalent to 9 per cent., is found between Archer and Old Irish.

Proceeding to the differences found in any one variety that are attributable to the effects of the season, the figures for Archer in

Comparison	No. of Tests	No. of Years	Total Nitrogen	Difference
(1) Archer, Goldthorpe	67	8	1·53 1·52	— ·01
(2) Archer, Standwell	24	4	1·56 1·64	+ ·08
(3) Archer, Scotch Chevallier	25	3	1·54 1·63	+ ·09
(4) Archer, Old Irish	15	2	1·55 1·69	+ ·14
(5) Archer, Hallett's Pedigree Chevallier	11	1	1·55 1·65	+ ·10
(6) Archer, Danish-Archer	12	1	1·51 1·47	— ·04

the same experiments, taken over a period of eighteen years, may be quoted. The number of tests of which the figures given in each year is the average, is shown in brackets :—

1901	1·51	(4)
1902	1·48	(6)
1903	1·65	(8)
1904	1·56	(10)
1905	1·55	(11)
1906	1·52	(12)
1907	1·55	(10)
1908	1·52	(8)
1909	1·47	(8)
1910	1·55	(6)
1911	1·60	(6)
1912	1·49	(3)
1913	1·26	(2)
1919	1·33	(6)
1920	1·76	(9)
1921	1·74	(8)
1922	1·64	(9)
1923	1·47	(7)
Average	1·54	

Here it will be observed that the largest deviations from the average occurred in 1913 and 1920, respectively, the former being ·28 below, and the latter ·22 above, the average—differences equivalent to $-$ 18 per cent. and $+$ 14 per cent., respectively. Both of these differences are much greater than that found between Archer and Old Irish. An important feature of the weather effect is that the differences brought about by this agency are not identical for every variety. In the British Isles neither very hot nor very cold weather, *i.e.*, weather producing rapid ripening on the one hand or long delayed ripening on the other, is conducive to good malting quality. But under conditions of excessive heat varieties characterized by a tendency to ripen slowly usually produce better malting grain than those with a tendency to more rapid ripening. Similarly, under conditions of long drawn-out ripening varieties with earlier ripening habits are superior in this respect.

In the same way, although a high state of soil fertility, especially if this is due to an excess of available nitrogen, is inimical to high malting quality in all varieties, it is less detrimental in some than in others.

Taking a series of seasons, an average figure for total nitrogen in malting barleys is 1·5 per cent. on dry matter. Barleys showing figures above this are approaching non-malting quality, whilst those below this average are classified as distinctly good.

The underlying ideas of improvement in the case of the barley crop are not dissimilar to those applicable to other crops, and centre upon attempts to increase the yield and to improve the quality of the grain concurrently. But of the three cereals barley undoubtedly possesses the weakest straw, so that in a very real sense improvement in this respect is not only desirable but necessary, especially where the fertility of the soil and other conditions under which the crop is grown are gradually assuming a more intensive character.

Finally, since the finest quality of malting grain is not obtainable where the crop is unduly long in ripening, there is general tendency in Western European countries to prefer varieties with early ripening habits.

In recent times the most important investigations of an economic nature with malting barley originated in Denmark. They consisted of a long series of variety trials carried out by the Royal Agricultural Society of Denmark and the Carlsberg Brewery of Copenhagen, who collaborated to the extent of ascertaining the malting and brewing capacities of the different varieties under experiment.

The barleys in most extensive use about the time the Danish experiments were commenced were narrow-eared forms, *Hordeum nutans*. In many cases these were strictly indigenous barleys of old standing which, although characterized by a general morphological conformity, exhibited diversified physiological attributes such as differences in times of ripening. In Scotland, for example, with its cool, moist climate, varieties were in use which succeeded well under those conditions. Similarly, varieties were found in the west and east of England which were adapted to the distinctive environments of those two districts, whilst in Ireland there was at least one "variety," Old Irish, which survives in use to this day. Old Irish is characterized by a distinct rapidity in vegetative development, and by earliness in ripening; the former feature enables it to compete with the rapid weed growth common to mild, damp climates, and the latter is an advantage where such conditions favour unduly protracted growth. Scattered over other parts of England and Wales there were many localized forms that were usually known by the name of the locality in which they were found, and similar conditions obtained in the barley-growing countries on the Continent.

About 1835, however, a barley named Chevallier after its introducer, the Rev. Dr. John Chevallier, of Aspall Hall, Suffolk, began to assume a leading position amongst varieties in the British Isles. It spread in time to the Continent and there became widely known under various names, either of localities or of persons. From the date of its introduction until about 1900, Chevallier occupied an important position as malting barley in Britain and on the Continent. It was not markedly more prolific than the old indigenous or land varieties, but in colour, shape and quality the grain exhibited a very definite advance on that of its pre-

decessors. The straw of Chevallier was moderately long, but not, however, particularly strong, and with the increased fertility of arable land, resulting from the more liberal use of artificial fertilizers towards the end of the nineteenth century, this defect became more evident.

As a result in part of the Danish and, later, of the Irish experiments, Chevallier was superseded by Archer. Botanically Archer belongs, like Chevallier, to the lax, narrow-eared group of two-rowed barleys. It is prolific, and its straw is shorter and better standing than Chevallier. So far as it is possible to judge from agricultural literature, Archer has existed in parts of southern England as an indigenous sort in an unselected condition for a very long time. Its high yielding potentiality was not appreciated beyond the bounds of the few districts in which it was grown until within recent times, but it has lately had a very wide circulation and, as will be seen later, has formed a basic variety in the improvement of the crop.

In addition to the narrow-eared barleys, *Hordeum nutans*, used for the production of malting grain, there were also a few broad-eared forms, *Hordeum erectum* and *Hordeum zeocrithum*, in use in the early part of the nineteenth century. These generally were of much less importance economically than the narrow-eared types until the advent of Goldthorpe in about 1890, which by reason of its high grain-yielding potentiality and its remarkably good malting quality, brought the cultivation of broad-eared types under consideration, both experimentally and commercially.

The Danish experiments began in 1883, and the varieties tested in that year were three native sorts, and various imported barleys from England, Scotland and France. Amongst the latter was a barley named Prentice, the seed of which was obtained from England. This barley was subsequently found to be identical with the variety known in England as Archer, the leading features of which have been outlined above.

The Danish variety tests were continued from 1883 to 1903, and the outstanding feature of these extended and widely distributed trials was that Prentice proved superior in yield to all the narrow-eared forms tested, whether indigenous or imported. Hardly less

important was the finding that although in appearance Prentice was not so attractive as Chevallier and many of the other varieties included in the investigations, its intrinsic quality, *i.e.* the quantity of extract it produced on brewing, was superior.

From the original unselected Prentice a considerable number of single plant selections was made in Denmark, and the most promising of these were propagated as distinct cultures. Such were Princess, Tystofte and Lyngby Prentice, to which others have been added from time to time. All of these exhibit a superiority in some direction or other to the original Prentice, but most commonly in the direction of quality, and to a lesser extent in yield.

A series of investigations very similar to the Danish was commenced in Ireland about 1900 by the Department of Agriculture there, in collaboration with Messrs. A. Guinness, the celebrated brewers. The latter, like the Carlsberg Brewery, carried out malting and brewing trials with the produce of the various experimental plots.

The general line of inquiry followed that adopted in Denmark—that is, commencing with indigenous Irish and promising foreign varieties, an effort was made to ascertain which was the most profitable for the farmer and at the same time most suitable for the brewer, and it is noteworthy that the variety finally decided upon as being the most valuable to both interests was Archer, or Prentice barley as it was known in Denmark.

Both the Danish and Irish experiments demonstrated that high malting quality and low total nitrogen content in the grain are synonymous terms, and that although brightness of the colour of the grain may be an indication of the conditions under which the crop is harvested, it is not necessarily an index of high malting quality. They also demonstrated that high yield of grain and high malting quality in a variety are not antagonistic attributes.

From the breeding point of view a very important result that has emerged is that total nitrogen in the grain is a varietal characteristic. Thus Archer has a lower total nitrogen figure than Chevallier, and the extended cultivation of this barley over large areas, which followed as the outcome of the investigations

just described, marks an undoubted advance for both the agricultural and brewing interests.

Although Archer is a variety of high grain-yielding potentiality, it is relatively late in ripening and the straw is somewhat weak, more particularly in seasons conducive to rapid vegetative development in the spring. The late-ripening tendency in this case is somewhat of a relative nature, and except in very wet, cool seasons it rarely proceeds to the extent of endangering the saving of the crop. Nevertheless, the tendency towards lateness in ripening becomes accentuated under such conditions, and the possibility of securing the highest malting quality is then correspondingly reduced.

The disadvantages arising from weak straw need no emphasis beyond the statement that in the case of barley the grain of a fallen or lodged crop may be seriously discoloured. Provided that the germinating capacity is not injured, the latter is a commercial rather than a necessarily intrinsic defect, but the total nitrogen content of the grain of a lodged crop invariably tends to be higher than that of a crop which remains erect until it is harvested. Moreover, the cost of the additional labour necessary to harvest a lodged crop may absorb the financial advantage accruing from enhanced yield.

As the result of many attempts to secure better straw combined with high grain yield and good quality, two varieties, Spratt-Archer and Plumage-Archer, were finally secured. The former, a narrow-eared variety, was produced by the writer by crossing Archer with Spratt, and the latter, a broad-eared barley (*erectum*), was produced by Dr. E. S. Beaven of Warminster by crossing Archer and Plumage. Spratt is a barley with very specialized uses. It is a variety of very old standing formerly grown extensively in the English Fen districts, where the soil is frequently a blackish loam, heavily charged with organic matter. On such soils Spratt stands remarkably well and produces heavy crops of somewhat inferior malting quality, but when sown on the more usual types of barley soil it produces indifferent crops. But on every description of soil Spratt is characterized by distinctly stiff, up-standing straw, and in this respect is undoubtedly superior to all other British varieties.

The barley selected from Spratt × Archer, and subsequently named Spratt-Archer, is very similar in ear shape to the parent Archer. It marks a distinct improvement on that variety, however, in several characters, for it is superior in grain-yielding capacity, is stiffer strawed, earlier in ripening, and the grain is rather brighter in colour. Also, when sown under comparable conditions with the parent Archer, the grain contains a lower percentage of total nitrogen, and consequently produces better results in the malthouse and a larger extract in the brewery.

The following figures of yield and total nitrogen content relate to the results of certain of the earliest comparisons of the parent Archer and the hybrid Spratt-Archer, carried out on two distinctly different classes of soil, and in two seasons. They serve to demonstrate the marked superiority of the new hybrid in point of yield, more particularly in the wetter year, 1919, and in point of quality on the heavier soil, Centre II, where the tendency to lateness in ripening would naturally be intensified.

Centre I (Light Land)

	Yield of Grain		Total Nitrogen	
	1918	1919	1918	1919
Archer I	207	181	1·48	1·41
Spratt-Archer 37/6 . .	223	200	1·38	1·29
Mean Difference .	16	19	0·10	0·12

Centre II (Heavy Land)

	Yield of Grain		Total Nitrogen % on Dry Matter	
	1918	1919	1918	1919
Archer I	211	185	1·73	1·46
Spratt-Archer 37/6 . .	225	233	1·53	1·27
Mean Difference .	14	48	0·20	0·19

In a great many cases other forms arising out of the cross Archer × Spratt possessed much better standing straws than Spratt-Archer 37/6, but these were almost invariably associated with high total nitrogen in the grain.

Of all malting barleys in use in Western Europe during the past quarter of a century, Goldthorpe has proved the most valuable qualitatively. It is, moreover, a variety with a high-yielding potentiality capable of growing crops that are satisfactory to both the brewer and the farmer on much heavier soils, and on soils in a higher condition of fertility, than those suitable to narrow-eared sorts. On the other hand, Goldthorpe is not equally suitable to light soils, especially in districts of limited rainfall. A serious limitation to the utility of this variety is the fact that the straw becomes very brittle when ripe, and the ear is then liable to become detached from it, thereby entailing losses of considerable magnitude in some seasons. Archer rarely suffers in this manner, for the straw of this variety in addition to being relatively shorter, is greatly strengthened by the uppermost leaf sheath which extends from the node to a relatively very short distance below the base of the ear.

In an attempt to obviate the losses sustained in this manner Beaven crossed Plumage barley, a form of Goldthorpe, with Archer, and ultimately secured a broad-eared form very similar to Archer in straw characteristics, which he named Plumage-Archer. Plumage-Archer retains all the high malting quality of the parent Plumage, combined with the high-yielding potentialities of both parents. Like Plumage, it is also fairly early in ripening and can thus be utilized in districts of lower mean temperature than Archer and Spratt-Archer. Plumage-Archer and Spratt-Archer are now the predominant varieties in the British Isles (Armstrong, 1928, Report on the Marketing of Wheat, Barley and Oats in England and Wales, 1928).

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CHAPTER III

OATS (*AVENA sp.*)

THE cultivated oats of the greatest economic importance are grouped under two species, *Avena sativa* L. and *Avena byzantina* Koch, the former a polymorphic species generally regarded as being derived from *Avena fatua*, the wild oat of cultivated land, and the latter a similarly polymorphic group originating from the wild oat, *Avena sterilis*, found in countries bordering on the Mediterranean. A third species, *Avena strigosa*, furnishes a series of oats cultivated to a considerable extent on land of fairly high elevation in Wales, and in a few islands off the west coast of Scotland.

Viewed as a whole, the varieties grouped under *Avena sativa* are grown in temperate climates, and succeed best under conditions of liberal rainfall, especially in the early periods of vegetative development. Such varieties are also usually characterized by relatively long periods of growth. In very many parts, more particularly in Western Europe, the straw is used for stock-feeding, and the crop therefore partakes of a dual-purpose nature.

Varieties classified under *Avena byzantina* are sometimes regarded as drought-resisting forms, but this description requires modification to the extent that, provided there is sufficient moisture to ensure early vegetative development, the later stages of growth can be successfully sustained, even with a severe limitation of rainfall. The oats in this group have also a relatively short period of growth, and are grown extensively in countries bordering on the Mediterranean, the western states of the United States of America, in South Africa, Australia, and in parts of South America—all areas of relatively low rainfall and high mean temperature. To some extent the short period of growth rather than actual ability to resist drought furnishes the reason for their

cultivation in these areas, as the crop is ready for harvesting early in the summer before the usual period of severest drought sets in.

Varieties of *Avena byzantina* have usually fine but not very abundant straw, which is not particularly good standing, at least under the conditions regarded as favourable for *Avena sativa*. *Avena byzantina* is the only species in which varieties with red husks (palea) are met with.

Trabut (1911) considers that many derivatives of *Avena sterilis*, in addition to being specially suited to southern countries, possess a marked ability to succeed on saline soils. The undoubted resistance of some derivatives of *Avena sterilis* to certain fungoid diseases is an attribute the value of which will be made evident later in the accounts of various breeding experiments.

By far the greater portion of the oat crop is utilized for stock-feeding, although large but decreasing quantities are still used as oatmeal for human consumption.

The caryopsis or true kernel of oats is invested by two paleæ which form what is commonly known as the husk, and constitute from 20 to 30 per cent. or more of the total weight of the whole grain. The quantity of the husk in an oat varies according to the variety, and, to a less extent, with the climatic conditions under which the crop is grown. The composition of the caryopsis of oats compared with that of wheat is :—

	Crude Protein	Crude Fat	Nitrogen-free Extract	Crude Fibre	Ash
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Wheat .	13·9	2·5	78·2	3·4	3·9
Oats. .	14·2	6·8	75·4	1·4	2·3

The most striking difference between the two cereals is the larger quantity of crude fat found in the oat.

The composition of oat husk may be stated as follows :—

Protein	Oil	Carbohydrates	Fibre	Ash
Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
2·1	0·81	55·7	35·8	5·2

And it will be observed that the high percentages of crude fibre and ash are here salient features.

Kellner (1915) gives the following figures for the composition of the three cereal grains as threshed :—

	Moisture	Crude Protein	Crude Fat	Nitrogen-free Extract	Crude Fibre	Ash
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Wheat .	13·4	12·1	1·9	69·0	1·9	1·7
Barley .	14·3	9·4	2·1	67·8	3·9	2·5
Oats .	13·3	10·3	4·8	58·2	10·3	3·1

The relatively high proportion of crude fibre in ordinary oats will be noted; most of this, as the first two analyses show, is derived from the husk of the grain; consequently since the quantity of husk is subject to a varietal variation, the importance of this attribute in the improvement of the crop will be realized.

Since the principal cultivated oats are derived from three species possessing definite degrees of adaptation to environmental conditions, it follows as a natural sequence that the lines of improvement pursued in different countries have distinct and separate objectives. For this reason these will be treated separately.

Europe

As already noted, varieties of *Avena sativa* as a group succeed best under conditions of moderate temperature and abundant rainfall. Of the cereals, oats are much more generally grown than barley and wheat, and the large number of varieties in use, in some cases even within very restricted areas, may be attributed in some measure to the wide diversity of conditions under which this crop is cultivated.

It is still a debatable point whether derivatives of *Avena strigosa* or of *Avena fatua* (*i.e.*, *Avena sativa*) were the first oats cultivated in Britain, but from material obtained from an excavated site at Fifield Bavant, in Wiltshire, Biffen (1925) came to the

conclusion that oats were cultivated in Britain at least in pre-Roman times.

Another form, Piley or Pilcorn (literally, peel corn, in reference to its huskless condition when threshed) (*Avena nuda brevis*), still seen growing occasionally in Southern Ireland, was well known in Tudor times.

Two of the earliest and well-authenticated improvements were provided by the advent of Potato oat in 1788 and of Sandy oat in 1824—both chance discoveries of single plants exhibiting exceptionally desirable features. Both varieties survive to the present, and as the grain is of good quality, and the straw abundant and especially suitable for stock-feeding, they are still utilized in Scotland and Northern Ireland, where their cultivation is particularly favoured by the moderately low mean summer temperature, and normally abundant rainfall.

Following these introductions a series of very good varieties was put on the market by Patrick Shirreff (1873) about the middle of the nineteenth century, Hopetoun and the Fellow family being the most notable of his selections.

In 1892, the hybrid oat, Abundance, obtained by crossing White August and White Swedish, was introduced by Messrs. Gartons of Warrington, and following this a long series of hybrid varieties has appeared at intervals.

Berry (1920) in a study of oat varieties gives the composition of no less than 120 seedsmen's varieties, together with their comparative yield of grain and straw. The figures he submitted in his paper show an increase in the grain-yielding capabilities of the newer varieties, combined with a tendency towards greater earliness in ripening, and this is found concomitantly with reduced production of straw, which, however, is generally better standing. Thus, to some extent, in securing higher grain-yielding potentiality the strongly marked dual capacity of the older established varieties, such as Potato, Sandy, Hopetoun and Fellow, has been lost.

The composition of the kernel also indicates a reduction in the amount of oil, and an increase in the amount of carbohydrate with the advance from the older to the more modern varieties.

In North-Western Europe, Probsteier oat has formed the basis of much of the improvement effected in the spring oat crop during the last thirty to forty years. This is an indigenous oat found at Probstei, in Holstein, and in its unselected condition consisted of a mixture of a great many yellow- and white-grained stiff-strawed types. The spikelets were mostly two-grained, but in some forms there was a tendency towards three-grainedness.

Systematic selection of Probsteier oat was commenced at Svalöf in 1892, and one of the most notable products obtained by this means was Victory, which was derived from Milton oats, a type of Probsteier, and put on the market in 1908. Golden Rain, another selection from the same stock, but a yellow-grained oat, was introduced five years before Victory. Victory oat has gained a very wide and general cultivation in West European countries, chiefly on account of its high grain yield and good standing straw, but in some measure also because of the generally high quality of the grain. It has practically superseded such varieties as Hvitling, White Probsteier and Ligowo, which were in general use in Scandinavian countries previous to its introduction (Åkerman, 1924).

The Swedish investigators found the Probsteier oat so polymorphic in character that they continued their search for superior forms for some time after the introduction of Victory. Crown oat, for instance, was isolated and introduced in 1914, and amongst others that are now well known commercially are Weibull's Fortuna, and the Danish varieties, Gul Næsgaard, Abed Nova and Tystofte Stjerne. None of these can be regarded as surpassing Victory, although some of them displayed superior suitability to certain definite conditions of soil and climate.

Gul Næsgaard was obtained by H. Vestergaard as a selection from Beseler's oat, which in turn was a German Probsteier variety, and is a high-yielding variety under favourable conditions. Vestergaard also selected Nova, in this case from a Danish Probsteier; Nova ripens a little earlier than Victory, to which it is approximately equal in yielding capacity.

Another variety originating from an indigenous sort is von Lochow's Gold Oat, which was obtained by selection from a German "land" sort from Barwalde; it has a stronger tillering

habit than Victory and other Probsteier derivatives, and rather longer, narrower grains. It appears also to be less exacting in the matter of the supply of moisture, hence, in tests in Sweden, it gave better yields and surpassed both Victory and Crown in the years 1915, 1917 and 1918, all of which were characterized by a dry spring and an early summer.

The chances of securing forms exhibiting marked superiority to Victory by further search amongst the forms of Probsteier grew gradually less, and recourse was at length made to hybridizations between Victory and Gul Naesgaard, and Victory and Golden Rain I. From the former, Svalöf King oat was produced and introduced in 1923 ; in general appearance King closely resembles Victory, but at Svalöf it exceeds that variety slightly in yield, and more definitely, in quantity of straw. From the latter, Golden Rain II was obtained ; it is superior in yielding capacity and in quality to Golden Rain I.

With regard to black-grained oats—an attempt was made at Svalöf to provide a variety that would ripen earlier than Stormogul —a selection from Black Tartarian oat—which, although characterized by high grain-yielding capacity, is too late in ripening in the Swedish districts devoted to black oats. In 1905, Nilsson-Ehle crossed Stormogul and the much earlier ripening Klock II (Bell II), and obtained a black oat, which was put on the market in 1917 as Klock III (Bell III). The new oat is as early as Klock II, but in yield of both grain and straw it is superior to that variety. A further variety, namely, Engelbrekts, was obtained from the same cross. This variety is distinctly early in ripening, and surpasses Klock III in yield of grain. It is so nearly equal to Stormogul in yield that the original object of producing a new form combining the high yield of Stormogul and the earlier ripening habit of Klock may be regarded as being attained.

It may be observed that neither Klock III nor Engelbrekts produces the same abundance of straw as the original parent Stormogul. Åkerman draws attention to the difficulty of obtaining a combination of high straw yield and earliness in ripening ; on the other hand, the varieties under immediate

discussion exemplify the combination of high grain yield combined with earliness in ripening.

It will be observed also that these conclusions, although they arise from considerations of a different aspect, conform with the earlier remarks on the general tendency of oat improvement in the British Isles, namely, that the older established varieties produced abundance of straw, but were late in ripening, whereas more modern varieties produce less straw and more grain, but are earlier in ripening. The observations made with regard to selections of *A. strigosa* (p. 68) are also apposite.

Recent plant breeding developments in Ireland exemplify improvements that have been obtained by directing particular attention to the standing power of the straw. Both the average rainfall and the average mean temperature are higher in that country than in Great Britain, and under these conditions an excessive vegetative development is induced, which is accentuated when the early part of the year is unusually mild. This frequently results in the crops becoming laid with heavy rain and wind, and even when the corn is not damaged thereby, the extra labour involved in harvesting increases the cost of production very greatly.

The earliest attempt to mitigate the tendency to "lodging" was made about 1912 by crossing Banner and Black Tartary oats, the former a white-grained form with an open panicle, and the latter a black-grained variety with a closed panicle; both varieties were distinctly strong-strawed.

From this cross a white-grained form was obtained with strong upright straw and white grain, which was introduced under the name White Cross. Later, further selections were made from this selection and one, ultimately named Glasnevin Sonas, has been introduced into general cultivation by the Plant Breeding Institute of the Seorstat Ministry of Agriculture. This oat has proved a considerable advance on its parents in both standing power and yield.

A further attempt with the same problem was made by crossing Black Tartary and Potato oats. In this case a black-grained selection, Black Potato, possessing unusually good standing straw,

was made from the hybrid progeny. Unfortunately this oat did not give a sufficiently high grain yield, and it was not put into general use. It was utilized, however, as a parent in the cross Black Potato × Victory and from this hybrid Mr. I. W. Seaton of the Plant Breeding Division of the Ministry of Agriculture of Northern Ireland has selected a form which has been introduced into cultivation as Stormont Arrow. This oat combines in a remarkable manner the good straw of Black Potato and the high yielding properties of Victory, and at the same time does not suffer unduly like so many stiff-strawed varieties from a high husk content.

In a series of comparisons made at thirty-three centres in Northern Ireland in the seasons 1929, 1930 and 1931, Stormont Arrow exceeded Victory in yield of grain and straw by 8 and 9 per cent. respectively. Similar comparisons made with Potato in the same period showed the new variety to be superior in yield of grain and of straw by 11 and 5 per cent. respectively. These differences represent a monetary superiority of 9 per cent. over Victory, and 11 per cent. over Potato. To a large extent the increase in yield may be attributed to a reduction of the losses ordinarily sustained by laid crops, but the monetary superiority quoted above does not take into account the greatly reduced cost of harvesting a standing crop—and this must be very considerable.

Avena strigosa. Oats belonging to this species are limited in their use as cultivated crops to Wales and the west of Scotland. They are important in those areas, for they can be cultivated at elevations greatly above those usually found appropriate to varieties of *A. sativa.* They also produce relatively large quantities of fine, long straw, which has a high value for stock-feeding.

Three main groups of *A. strigosa* have been described and defined as sub-species, namely: *pilosa*, *glabrescens* and *Orcadensis*, the differences between which have been based on the degree of hairiness of the dorsal palea. (Marquand, C.V.B., 1922.) In *pilosa* the dorsal palea is completely covered with long, stiff ascending hairs; in *glabrescens* the palea is glabrous throughout its length; and in *Orcadensis* the palea is covered with stiff ascending hairs in its upper portion and glabrous in its lower.

As found in cultivation each of these sub-species is a collection of an indefinite number of forms varying in their total productivity of grain and straw, and of grain and straw separately. They also exhibit real differences in standing power, and in earliness in ripening. In these circumstances the first method of improvement that suggests itself is the selection and individual propagation of separate plants exhibiting desirable characters. The adoption of an adequate basis for selection is somewhat difficult, as it involves an evaluation of characters that are apparently antagonistic. Thus, varieties that are late in ripening generally produce heavier yields of straw than those of earlier maturing habit. Again, it is found that slower growing forms are hardier than more quickly growing forms, and that under the conditions in which *A. strigosa* is cultivated, early varieties produce better samples of grain than late ones. Late varieties, however, can withstand adverse conditions experienced during growth better than early ones.

Despite the conflicting tendency of these attributes, it has been possible to select a line of each sub-species that is superior in total yield (*i.e.*, grain plus straw) and in yield of straw and grain respectively to a check which was an aggregate of the Ceirch Llwyd variety. Several of these superior lines have been developed and introduced into general cultivation (Jones, 1931.)

America

Oats, like wheat and barley, originated in Europe, Asia and Northern Africa and the earlier progress in the development of the oat crop in the United States and Canada is attributable to the introduction of varieties from foreign sources. Individual lots of these introductions increased in importance as their suitability to their new conditions of environment was established, and within recent times the best of them, which were doubtless aggregates of variations, have been subjected to selection whereby a large number of superior forms has been obtained.

Oats are the third most important cereal crop and rank fifth in value among the farm crops of U.S.A. The States leading in the production of oats are Illinois, Iowa, Wisconsin, Minnesota and Nebraska ; there are also considerable areas found in Indiana,

Ohio, New York, Michigan, Pennsylvania, North and South Dakota, Kansas, Texas, Missouri and Oklahoma.

The oat-growing area of the United States for the present purposes, however, may be divided into a northern and southern region. In the relatively cooler, northern regions varieties of *Avena sativa* are predominant, whilst derivatives of *Avena sterilis* are utilized extensively in the warmer western and southern regions; thus the improvement of the oat crop in the United States of America comprehends work on two species.

In the United States in 1919, types of oats describable under Silver Mine and Red Rustproof, both belonging to *Avena byzantina*, occupied the first and second positions of importance, respectively, on an acreage basis. The third position was occupied by Kherson or Sixty-Day (*Avena sativa*), and such selections therefrom as Albion, Iowar, Gopher, Richland and States Pride (Coffman and Stanton, 1925).

Kherson is the most important spring oat in the white oat region. It is usually linked in nomenclature with Sixty-Day and has been fully described by Warburton and Stanton (1920), who found no botanical distinction between the two varieties and therefore regarded them as synonyms. Kherson was obtained from Russia in 1896 by the Nebraska Experiment Station through the agency of Professor F. W. Taylor, and Sixty-Day from Dr. S. de Mrozinski of Proskurov in 1901. The fact that the stocks of seed of the two varieties were obtained from adjoining provinces in Russia is confirmation of their common origin.

Kherson or Sixty-Day is a yellow-hulled, short-strawed oat of good quality. It is decidedly early, for it ripens in from 90 to 100 days from sowing, or approximately 10 to 15 days earlier than most other spring varieties of *Avena sativa*. Because of this earliness, Warburton and Stanton state "it is enabled to escape to some extent injury by drought, storms and Rust." From an extended series of trials these investigators conclude that Kherson yields well in most of the spring oat sections of the United States. Where mid-season varieties can be grown successfully, however, they out-yield Kherson, but under drier climatic conditions Red Rustproof, Burt and other derivatives of *Avena sterilis* are superior.

It was found that there was a commercial discrimination against Kherson on account of its yellow grain, and from this circumstance there arose a demand for an oat with a white grain, but possessing the other valuable agricultural characters of Kherson. The fact that Kherson contained a considerable number of variations had been known for some time (Coffman and Stanton, 1925), and in 1906 a white grain single plant selection was made by Burnett (1925) at the Iowa Agricultural Experiment Station. This oat, which was named Albion and was white grained, although not superior to Kherson in yield, became very popular and is now largely grown.

Three further selections from Kherson, namely, Richland (1906), Iowar (1910), and Iogold, were made by the same cerealist. Richland, an early yellow oat, was selected on account of its short, stiff straw; it is superior to both Kherson and Albion in yield of grain, and, because of its stiffer straw, is more suitable than those varieties on richer soils where the crop is liable to lodge.

Iowar, a white-grained variety, was selected from Kherson in 1910 and has a taller straw and is a little later than Albion. It is superior to Kherson and Albion in yield of grain, and as it also produces more straw than the latter, it will probably replace it.

Iogold, a yellow-grained variety, was raised as a single plant selection from Kherson in 1906 and distributed to growers in 1927. It is stiffer-strawed than Iowar, to which variety it is at least equal in yield of grain, and in 1926, in which year there was an epidemic of Stem Rust, it exhibited a high degree of resistance to that disease (Burnett, 1928).

One selection from Sixty-Day, namely Gopher, may be mentioned. This was made at the University Farm, St. Paul, Minnesota, in 1917 and is now an important commercial variety in Minnesota: it is a white-grained, early-ripening variety with good straw and high yielding capacity.

Swedish Select, which belongs to the *Avena sativa* group, is one of the oats of European origin that have been found suitable to conditions prevailing in certain regions in the United States of America. It was introduced into that country by M. A. Carleton (1910), by whom it was obtained in Russia in 1899. It originated,

however, in Sweden and from there found its way into Finland and some of the north-east provinces of Russia. Swedish Select is described as a mid-season variety, and is suitable for regions between the Great Lakes and the Rocky Mountains ; it has been particularly successful in Wisconsin.

To a very considerable extent the improvement of what are commonly known as red oats, that is, derivatives of *Avena sterilis*, centres around two varieties, Burt and Fulghum. Burt, which has been studied at some length by Coffman, Parker and Quisenberry (1925), is stated to have originated as a selection from a field of Red Rustproof about 1878. No account of the origin of Red Rustproof is offered, but it would probably originate, as all the other parent stocks of this cereal in America have done, in parcels of seed from Europe. These investigators demonstrated the polymorphous condition of Burt oat then in use ; it evidently consisted of a very large number of variants, many of which exhibited desirable economic features, and some of these have been increased in quantity and distributed amongst growers.

Fulghum is a variety of the red oat group, *Avena byzantina*, that was selected about thirty years ago from a crop of Texas Rustproof by Mr. J. A. Fulghum of Warrington, Georgia, on whose farm the crop was growing. The single plant, which appears to have produced five heads, was conspicuous by reason of its greater height, and by the fact that at the time it was first noticed it was riper than the majority of the plants composing the crop. The grains are plumper than those of Burt oat, and, in addition, usually awnless, and the callus hairless (Stanton, 1921).

Its earliness, good yielding capability and high quality are important agricultural features. Fulghum also exhibits a marked resistance to both Smuts (see pp. 72–73), but is extremely susceptible to both Stem Rust and Crown Rust (see pp. 73–80).

A strain of Fulghum which reached the Kansas Agricultural Experiment Station in 1917 under the name of Nicholson's Improved Extra Early Red Rustproof, proved extremely promising, and as it was found to originate from Georgia, where Fulghum was first obtained, it was originally distributed to

farmers in 1911 under the name of Kansas Fulghum, but later it was re-named Kanota. Kanota outyielded the selections of Fulghum then in use at Manhattan and also exhibited a marked degree of resistance to both Smuts (Salmon and Parker, 1921).

Smuts. Further discussion of these and similar varieties leads to the question of the fungoid diseases of oats, the most serious of which are Loose and Covered Smut, *Ustilago avenæ* (Pers.), Jens., and *Ustilago levis* (K. and S.), Magn. ; Crown Rust, *Puccinia lolii avenæ*, McAlpine ; and Stem Rust, *Puccinia graminis avenæ* Eriks and Henn. These diseases appear to be particularly destructive in the United States and Canada, and their incidence and the possibility of obtaining varieties resistant to them have been the subjects of a great deal of research there in the last few years.

G. M. Reed (1920) published the results of a series of inoculations of oats with Powdery Mildew, Crown Rust, Loose and Covered Smuts continued from 1914 to 1919. The question of the Smuts will be considered first ; one hundred and fifty-four varieties and strains of oats were tested for their reaction to Smut during the period mentioned, and in these tests the following gave consistently negative results :—

Avena brevis.
Avena strigosa.
Avena sativa var. Black Mesdag.
Avena sativa var. Nigra.

Most derivatives of *Avena sterilis*, especially Burt, Early Ripe, Fulghum and Selection, gave low percentages of infection and the *Avena nuda* group proved highly susceptible.

Reed, Griffiths and Briggs (1925) published a further report on a more extensive series of Smut infection experiments that corroborated this earlier work in a striking manner. Thus, of six strains of *Avena brevis* five gave negative results ; the remaining strain was later in maturing and differed from the other five strains in other respects. Four plants out of 1016 were infected with *U. levis* and 8,508 plants gave negative results with *U. avenæ*.

Four strains of *Avena strigosa* were used and no infection with

either *U. avenæ* or *U. levis* was obtained in a total of 8,560 plants.

Two hundred and seventy-two varieties and strains of *Avena sativa* exhibited great variation in their susceptibility, but Black Mesdag, Culberson, Caucasus, Danish Island and Siberian proved very resistant. On the other hand, some proved highly susceptible, but the largest number appeared in a group between these extremes. In some cases varieties exhibited a higher susceptibility to *U. avenæ* than to *U. levis*, but in a few instances the reverse was the case. All varieties of *Avena sativa orientalis* were susceptible.

Whilst the wild forms of *Avena sterilis* were moderately susceptible to both Smuts, cultivated forms such as Burt, Fulghum and Red Rustproof exhibited a marked resistance thereto.

Three strains of *Avena fatua* were susceptible and seven strains of *Avena nuda* were highly susceptible to both Smuts.

Markton, a mid-season, yellowish-white grained oat, may be mentioned here (Stanton *et alii*, 1924). The source of origin of this variety is Dedeagatch, Turkey, whence a quantity of seed was obtained from which a selection was made at the Sherman County Branch Station, Moro, Oregon, in 1911. Markton is noteworthy as being immune from Covered Smut and is, in addition, a heavy-yielding variety. Levine *et alii* (p. 75) in certain Smut experiments conducted in 1925 notes that Markton is very resistant to both Smuts. As will be seen shortly, however, Markton is very susceptible to attacks of both Stem and Crown Rust.

Rusts. Two oat Rusts are common in the United States of America—Stem Rust (*Puccinia graminis avenæ*, Eriks and Henn) and Crown or Leaf Rust (*Puccinia lolii avenæ*, McAlpine). Stem Rust is more common in the northern and Crown Rust, although almost invariably present in the north, appears to be more abundant in the southern States.

To some extent the use of early-ripening varieties such as Kherson and its derivatives provide a protection in so far as they may by their earliness be rust-escaping, but a full measure of protection is believed to depend upon the ultimate provision of true drought- and rust-resisting varieties. A study of varieties from

this aspect has accordingly been pursued at considerable length. Parker (1918) found from a series of greenhouse tests that unquestionable resistance to Stem Rust was present in two varieties only, namely, White Tartarian and Ruakura Rustproof; the latter also gave evidence of some degree of resistance to Crown Rust.

Several varieties of *Avena byzantina* including strains of Burt, Cook, Appler, Italian Rustproof, Red Rustproof and Turkish Rustproof, are very resistant to Crown Rust, but none of the varieties of this group is resistant to Stem Rust. But Rust resistance is specific, for many of the varieties that are resistant to Crown Rust are highly susceptible to Stem Rust under identical conditions.

Levine, Stakman and Stanton (1930) give a detailed report of an extensive series of experiments at sixty-five Experimental Stations, extending over a period of five years (1923–1927). These investigations were designed to determine the degree of resistance of varieties of oats to the two Rusts under field conditions, and to ascertain and determine the identity of the physiologic forms of Stem Rust in the different experimental regions.

It was ascertained from these investigations that several varieties proved generally resistant to Stem Rust. The most resistant varieties are the following given in the order of their resistance :—

(1) Iogold, *Avena sativa* (early yellow).
(2) Hajira, *Avena sativa* (early yellow).
(3) Richland, *Avena sativa* (early yellow).
(4) Minota × White Tartary, *Avena sativa* (mid-season white).
(5) White Tartary, *Avena sativa orientalis* (late white).
(6) Green Mountain, *Avena sativa orientalis* (late white).
(7) Anthony, *Avena sativa* (mid-season white).

No variety exhibited a degree of resistance to Crown Rust corresponding to that found to exist in some varieties to Stem Rust, but the following were somewhat more resistant than the other varieties :—

(1) Green Mountain, *Avena sativa orientalis* (late white).

(2) Red Rustproof, *Avena byzantina* (mid-season red).
(3) Iowar, *Avena sativa* (early white).
(4) Rustless Selection, *Avena sativa* (early white).
(5) Burt, *Avena byzantina* (early red).
(6) Ruakura, *Avena sativa* (early grey).
(7) Hajira, *Avena sativa* (early yellow).

It is apparent, as the authors of the Bulletin referred to point out, that there is no general correlation between resistance to Stem Rust and resistance to Crown Rust; thus, whilst Iogold was the most resistant to Stem Rust, it was amongst the most susceptible to Crown Rust. Nevertheless, one or two varieties, namely Green Mountain and Hajira, are highly resistant to Stem Rust and are amongst the most resistant to Crown Rust also.

With regard to the combination of resistance to Smut and Rust, the following abstract from Bulletin No. 143 summarizes a highly interesting position, but one that at the same time renders the attempt to breed varieties resistant to particular fungoid diseases to which oats act as a host, difficult :—

" Unfortunately, there appears to be no correlation whatever between smut resistance and resistance to the rusts. For example, Markton and Fulghum were very resistant to both smuts, but extremely susceptible both to stem rust and crown rust. Red Rustproof also was highly resistant to both smuts and also to crown rust, but was very susceptible to stem rust. On the other hand, Green Mountain was susceptible to both smuts, but resistant to both rusts; and Anthony was very susceptible to the smuts and to crown rust, but resistant to stem rust. Again, Raukura was very susceptible to the smuts and to stem rust, but resistant to crown rust. Hajira was the only variety which appeared to be resistant to both smuts and both rusts.

" The smuts can be prevented by seed treatment, but it would be highly desirable to combine rust resistance and smut resistance in one variety, if possible. To do this probably will necessitate a detailed study of the number, distribution, and constancy of the physiologic forms of the smut fungi as well as the rusts. The results presented emphasize the fact that there is not necessarily

Varieties markedly resistant to *Puccinia graminis avenæ.*
Puccinia coronata avenæ.
Ustilago avenæ.

Puccinia graminis avenæ	*Puccinia coronata avenæ*	*Ustilago avenæ*	*Authorities.*
Iogold	Green Mountain	Red Rustproof	(*R.*, *G.* & *B.*)
			(*L.*, *Stk.* & *Stn.*)
Hajira	Red Rustproof	Burt	(*R.*, *G.* & *B.*)
			(*L.*, *Stk.* & *Stn.*)
Richland	Iowar	Hajira	(*L.*, *Stk.* & *Stn.*)
Minota × White Tartar	Rustless Selection	Fulghum	(*R.*, *G.* & *B.*)
			(*L.*, *Stk.* & *Stn.*)
White Tartar	Burt	Black Mesdag	(*R.*, *G.* & *B.*)
Green Mountain	Ruakura	Markton	(*L.*, *Stk.* & *Stn.*)
Anthony	Hajira	Culberson	(*R.*, *G.* & *B.*)
Edkin		Caucasus	(*R.*, *G.* & *B.*)
		Danish Island	(*R.*, *G.* & *B.*)
		Siberian	(*R.*, *G.* & *B.*)

L., *Stk.* & *Stn.* = Levine, Stakman and Stanton.
R., *G.* & *B.* = Reed, Griffiths and Briggs.

any correlation in the resistance of varieties of oats to different diseases."

In view of the limited degree of resistance to Crown Rust observed in the investigations up to the present, especial interest attaches to the discovery of a variety named Victoria. This variety was inoculated with each of eight biologic forms of Crown Rust both in the seedling and in the mature stages. In every case it exhibited marked resistance. Victoria was obtained from the province of Buenos, Argentina. According to Murphy and Stanton (1930), it possesses some of the characteristics of both *sativa* and *byzantina* oats, for the straw and palea exhibit the reddish-yellow colour associated with varieties classed under the latter, but the florets become detached as in varieties under *Avena sativa.* They suggest that the variety may have originated as a hybrid between these two species.

Another variety, *Avena strigosa* var. Glabrescens, showed a resistance equal to Victoria, and was resistant to all except one of the eight physiologic forms.

The results of the determination of the resistance of varieties of oats to Smut and Rust in America and Russia exhibit a striking similarity. Vavilov (1918) found only one variety of *Avena sativa,* namely, Mesdago, a brown-grained form (*Avena diffusa,* var. Montana Al) resistant to Loose Smut. This is most probably the same variety as is known in America and elsewhere as Black Mesdag (*see* p. 80).

Of four varieties of *Avena strigosa,* three were immune from Smut; one variety of *Avena brevis* and two varieties of *Avena byzantina* also proved immune.

One variety of naked oats (*Avena nuda* L. var. Biaristata, A. S. and Gr.) exhibited resistance to Loose Smut, but a second form was susceptible. Varieties of *Avena fatua* and *Avena Ludoviciana* are susceptible. The one variety of *Avena strigosa* that proved susceptible to Loose Smut was shown by Vavilov to be genetically different from other races of this species. One variety of *Avena barbata* was immune from Loose Smut; in two other varieties the stamens only were affected, and one variety was fully susceptible.

To Crown Rust, out of 323 sorts of *Avena sativa* only five proved relatively very immune; these were all sorts with coloured paleae. All varieties of *Avena fatua*, *Avena Ludoviciana* and *Avena sterilis* were very susceptible; *Avena brevis*, *Avena strigosa* and *Avena nuda* (L. var. Biaristata) were relatively immune.

To Stem Rust, out of 350 sorts examined only two races of *Avena sativa* proved relatively immune. One of them, the more resistant, belongs to var. Brunnea Kocke; the other, the less resistant, to var. Montana—two varieties with dark-coloured palea. All the other cultivated and wild varieties belonging to six species were badly attacked.

It will be noted that the varieties exhibiting immunity or strong resistance to fungoid diseases are included in the two species *Avena brevis* and *Avena strigosa*, both of which contain 7—14 chromosomes and neither of which will produce fertile hybrids with the species of *Avena sativa* and *Avena sterilis* which contain 21—42 chromosomes or with varieties of *Avena fatua* and *Avena Ludoviciana*, 21—42 chromosomes. The production of improved varieties from inter-species crosses in the case of oats is at present, therefore, impossible.

The whole position of the determination of the resistance of varieties of oats, as well as of other cereals, to fungoid diseases is still further complicated by the fact that the diseases may consist of distinct physiologic forms and that each such form may display a distinct virulence of attack. Point is lent to this observation in a report published by the Welsh Plant Breeding Station in 1923 (Preliminary Investigation with Oats, Welsh Plant Breeding Station, 1923).

Covered Smut, *U. levis*, was recorded on *A. nuda* var. Chinensis; *A. strigosa*, sub-sp. *glabrescens*, ex Welsh strigosa; *A. strigosa*, sub-sp. *Orcadensis*, ex Orkney strigosa. Only one specimen of Smut was found on the Welsh strigosa, but it was abundant in the Orkney form.

From an infection experiment made in 1922 with *U. levis* from Orkney strigosa, the Orkney plant was again infected, but none of the other varieties, Algerian sterilis, Welsh strigosa,

Ceirch-du-Bach, Black Tartary, Golden Rain, Radnorshire Sprig and Potato was infected. As the writers of the Report note, all these varieties were heavily infected with Loose Smut.

Reed (1924) published the results of a series of inoculation tests with *U. avenæ* and *U. levis* drawn from specimens obtained from Missouri and from Wales. The species and varieties tested included *A. brevis*, *A. nuda* (L. var. *inermis*) and *A. sterilis* (var. Fulghum and var. Red Algerian), lines of *A. strigosa* and varieties of *A. sativa*.

Ustilago avenæ from Missouri gave very heavy infection of *A. nuda, var. inermis*, and of three sub-species of *A. strigosa*; it failed to infect *A. brevis*.

Ustilago avenæ from Wales failed to infect *A. nuda* at all severely, also the Welsh varieties of *A. strigosa*.

Ustilago levis from Missouri caused a slight infection of *A. brevis*, but infected *A. nuda*, the Welsh forms of *A. strigosa*, and almost all other varieties of *A. sativa* severely.

Ustilago levis from Wales produced 100 per cent. infection of *A. brevis*, and of the Welsh forms of *A. strigosa*. Excepting in the case of Victor, it produced a negative result on all the sativa varieties.

It is noteworthy that Black Mesdag (*A. sativa*), Fulghum and Red Algerian (*A. sterilis*) gave negative results throughout.

A further contribution to this subject was made by Reed in 1930. He found eleven specialized races of Loose Smut and five races of Covered Smut differentiated on the basis of their capacity for infecting varieties of oats. All collections were capable of infecting *Avena barbata*, and one race of *U. Avenæ* is capable of attacking this species of oats only.

No race of Loose Smut has shown any capacity for attacking *A. brevis*. All the races of Covered Smut except No. V are capable of infecting this species, but only Race No. II produced a severe infection. In the case of all the other races only a few plants were smutted, and these to a small extent only.

Of the varieties of *A. sativa*, Black Mesdag and Markton are the only two varieties exhibiting a conspicuous resistance to all races of both Smuts. The other varieties of *A. sativa* and those of

A. nuda, *A. orientalis*, *A. sterilis* and *A. strigosa* showed varying degrees of susceptibility. Black Norway, Early Gothland, Green Russian, Nebraska No. 21, Rosoman, Scottish Chief and Tripserma were unusually resistant to all races of Covered Smut, although extremely susceptible to one or more distinct races of the Loose Smut.

Monarch and Joanette, on the other hand, were more susceptible to the Covered Smut races.

There were shown to be sharply defined races of Loose Smut capable of attacking varieties of *A. sterilis*, one exhibiting a peculiar capacity for infecting Fulghum and another for infecting Red Rustproof. No well-defined race of *U. levis* was capable of attacking any varieties of this species.

In view of the marked resistance of Mesdag to both forms of Smut, and in a high degree to Grey Spot, which will be discussed shortly, some note of its origin may not be without value and interest here.

According to Professor Rhodin (1908), Mesdag originated in Holland, but is not known there under that name. The parent variety is President, an indigenous Dutch variety, and it was this unselected variety that was submitted to a process of selection by Messrs de Vilmorin, Paris. The form selected eventually from this population was named Mesdag, after a town in Holland, by Messrs. de Vilmorin.

The most striking features of Mesdag, according to Rhodin, were its earliness in ripening, and, as a result of this characteristic, its relatively high value in cold seasons and in seasons of heavy rainfall. Rhodin also mentions that when introduced into Finland, which is a country with a short season, Mesdag proved particularly useful.

Nilsson-Ehle, Holmgren and Åkerman (1921–22), in describing the character and origin of Mesdag, drew attention to a report by Dr. Koslag of Wageningen, Holland, who, like Rhodin, regards President, or more correctly Black President, as the parent stock, but claims that the name of the oat originated from a grain dealer of Gronigen, named Mesdag. It is stated further that President oat is not a truly indigenous Dutch variety, but that it arose from a

small parcel of seed introduced from a foreign source, probably the Baltic Provinces, about 1870.

The manner of inheritance of resistance and susceptibility to oat Smuts has formed the basis of a great many genetical studies. Reed (1928) records the results of crossing various susceptible and resistant varieties, etc. Thus, in the cross

Hull-less Oat × Black Mesdag
(susceptible to both Smuts) (resistant to both Smuts)

resistance was dominant to both Smuts.

In Silver Mine × Black Mesdag
(susceptible to both Smuts) (resistant to both Smuts)

resistance to both Smuts was again dominant.

In Canadian × Victor
(susceptible to both Smuts) (susceptible to both Smuts)

the progeny was readily attacked by both Smuts.

In Early Gothland × Victor
(susceptible to *U. avenæ* resistant to *U. levis*) (susceptible to both Smuts)

the progeny was 100 per cent. susceptible to *U. avenæ* and resistant to *U. levis*.

In Monarch × Hull-less
(resistant to *U. avenæ* susceptible to *U. levis*) (susceptible to both Smuts)

the progeny was susceptible to *U. levis* and resistant to *U. avenæ*.

Reed concludes from these experiments that there is no insuperable obstacle to obtaining resistance combined with desirable agricultural characters.

Gaines (1925) in his remarks on certain crosses with Markton states: "Data on F_3 families of Markton × Large Hull-less and Markton × Banner grown at Pullman, Washington, in 1926, and as yet not completely analysed, show the immunity of Markton to be dominant, but controlled by multiple factors—probably three."

Coffman, Stanton, Bayles, Wiebe, Smith and Tapke studied a series of crosses of Markton and a number of varieties susceptible to *Ustilago levis*—Early Champion, Ligowo, Scottish Chief,

Swedish Select, Iogren, Aurora—and express some doubt of the existence of three factors for resistance to all *Ustilago levis* strains in Markton.

Transgressive segregation for Smut infection was observed, however, in some F_4 lines of Markton × Scottish Chief and Markton × Swedish Select, the infection percentages in these cases exceeding those of the susceptible parents.

These investigators found little or no evidence of correlation between morphological characters and resistance to Smut infection and in this conclusion they are in close agreement with Reed (*vide* p. 81). In these particular tests the husks of the oats were removed and the inoculations were made by blackening the caryopsis thoroughly with Smut spores. Despite this treatment Markton proved "extremely resistant, if not actually immune, from the *Ustilago levis* strain used in these experiments."

The authors lay emphasis on the possibility of seasonal and place variations in Smut infection and also the necessity of limiting the conclusions to the Smut strains used.

Further evidence of the nature of the inheritance of resistance to *Puccinia graminis avenæ* is furnished by Deitz (1928). This investigator found that on crossing White Tartar, which is resistant, with National and Lincoln respectively, resistance was dominant. He also crossed three lines of Burt with White Russian; in two cases the F_1 was susceptible and in the third it was resistant to Rust. Again, in the case of Green Russian × Richland and in White Russian × Ruakura, the F_1 generation exhibited resistance. The F_2 produced some plants that were more resistant than either parent.

In addition to the losses the oat crop sustains as the result of the attacks of fungoid diseases, it is liable to severe damage arising from insect pest attacks, of which Frit Fly is the most serious in Europe. The manner of attack and the nature of the damage are briefly as follows: the fly winters in the larval stage in the stems of wild grasses, whence it passes to the oat crop in the spring. Eggs are laid either on the soil in close proximity to the plant, or on the plant itself, and the larva finds its way to the growing point of the one or many shoots (tillers) of the plant by

PLATE III

Specimen plant of (*left*) autumn-sown Grey Winter, and of (*right*) Argentine removed from the soil at the end of March, 1929. These two varieties are being used as parents in an attempt to secure new varieties of winter oats with better standing straw. It will be observed that Grey Winter has survived the winter conditions successfully, whereas the Argentine has succumbed (*see p.* 83).

[*To face p.* 82.

burrowing there directly or by travelling between the various leaf tissues. Once arrived there the larva sustains itself on the rich and succulent material of the growing point, which in consequence is usually completely destroyed, and the shoot thereby rendered useless. This loss stimulates further tiller production, but such tillers are usually too late in forming to develop into shoots of normal size; in any case they are unduly late in producing grain, and this is limited in quantity and frequently deficient in quality. Frequently the plant does not advance further than the mere proliferation of new tillers which never develop beyond a few inches in length.

No variety is immune from attack, but a few varieties have been shown to possess a high degree of resistance to attacks of the fly. Some varieties, moreover, exhibit a greater power of recovery after attack, whilst the very large number of tillers produced at an early stage in the development of the plant in others minimises the probable extent of ultimate damage.

It has been found that certain Scandinavian varieties, namely, Summer, Spet and Hede, are more resistant to the ravages of Frit Fly than Victory and oats of that class, and efforts made by Cunliffe to produce improved varieties from crosses between what may be regarded as resistant and non-resistant forms are already in an advanced stage (1929 and 1930).

The varieties of oats classified as true winter forms are usually characterized by high tillering capacity; further, the tillers, when the crop is autumn sown, are too far advanced by the time of the arrival of the fly in the spring to suffer serious damage. The use of winter varieties may thus provide an indirect means of securing some mitigation of the losses frequently suffered, and efforts are being made to secure new varieties with better standing straw than that invariably associated with the varieties which exhibit the highest degrees of winter-hardiness.

A trouble which may assume serious importance in oats is Grey Spot (Dörrfleckenkrankeit). Recent work points to certain abnormal soil conditions rather than to a parasite as the ultimate cause. The trouble, which results in severe damage to the leaves,

leading in extreme cases almost to defoliation, is found mostly between the fourth and fifth leaf-stage, and before the plant has commenced to show definite flowering shoots. Grey Spot appears most commonly on soils rich in lime and other alkaline fertilizers, and is countered by acid fertilizers such as ammonium sulphate, whilst manganese salts also check it.

The condition is most abundant in dry springs, but with favourable weather, *i.e.* an abundant rainfall, plants that are affected may recover completely, but in dry seasons the effects are discernible throughout the entire life of the plant.

Some investigations carried out by Nilsson-Ehle (1911) early in the century showed that varieties of oats differ in the degree to which they are resistant to Grey Spot. Some, such as Dala and certain varieties of *Avena sativa orientalis*, were specially susceptible, whereas Fyris, Mesdag, Danish Grey Oat, Spet, and some selections from German Moss oats were resistant. The Probsteier group of varieties, Golden Rain, Victory, Ligowo, suffered severely; Bell I and II and Stormogul were less affected.

These observations were confirmed later by Åkerman (1923–24) who classified many of the generally known varieties into four groups: (1) very susceptible, (2) susceptible, (3) resistant, (4) very resistant, as follows :—

(1) Black orientalis types; Svalöf Dala, Odal (Golden Rain × Dala), von Lockow's Yellow Oat.

(2) Probsteier, Victory, Crown, King, Nova, Golden Rain, Eko, Orion.

(3) Bell II and III, Engelbreckt, Stormogul.

(4) Fyris, Pearl,[1] Meloj III.[1]

Mesdag is placed between (3) and (4).

Davies and Jones (1931) classified certain varieties grown in Wales in 1929 as follows :—

Resistant . . .	Scotch Potato.
Highly resistant . .	Radnorshire Sprig
	Ceirch-du-bach.

[1] Norwegian varieties bred by Dr. Christie.

PLATE IV

Specimen plants of two selections from the hybrid Grey Winter × Argentine, removed from the soil on the same date as the parent plants shown in Plate III. Both these selections exhibit a high degree of winter hardiness and better standing straw than the parent Grey Winter.

[To face p. 84.

Moderately susceptible .	Victory.
	Record.
	Black Tartar.
Very susceptible . .	Orion.

They also drew attention to the marked reduction in the yield of plants on affected areas, and showed that the application of manganese sulphate to the soil gave complete control of Grey Spot.

Åkerman has also shown that segregation into resistant and susceptible forms occurs on crossing varieties differing in their reaction to Grey Spot.

Thus, in 1921 the F_1 plants obtained from the crosses Odal × Fyris and Ligowo × Bell II remained undamaged. Control plants of the two resistant varieties, Fyris and Bell II, likewise exhibited no trace of Grey Spot, but Odal and Ligowo III showed damage just as they had done in previous tests. It appears, therefore, that the resistance of Fyris and Bell II was dominant in these crosses.

In the same year Åkerman was able to study the manner of segregation in the F_2 and F_3 generations of a cross between Abed Nova and Bell III. In this case he regarded the evidence as indicating transgressive segregation, for some lines showed more damage than the less resistant Nova parent, whilst others were completely undamaged and therefore apparently possess a higher resistance than the Bell III parent.

To strengthen these conclusions, Åkerman draws attention to the occurrence of severely damaged and undamaged lines in close contiguity—an additional indication of the dependence of differences on genetical factors rather than on conditions of environment.

The occurrence of Grey Spot may be restricted to certain soil types with well-defined characteristics ; nevertheless, the knowledge of the existence of varieties with a distinct resistance to the trouble has provided a means of protection. That such resistance has a genetic basis also makes it possible to secure resistant varieties possessing other valuable agricultural features by hybridization.

From the various investigations of the behaviour of species of oats towards special parasitic fungi it has been shown that the greatest resistance to infection is found in *A. strigosa* and its sub-species *A. brevis*, to a slightly less degree in *A. barbata*, and in the sub-species macrocarpa of *A. sterilis*. Although individual varieties of *A. fatua* spp. sativa, exhibit some degree of resistance to certain parasitic fungi, this sub-species as a whole is characterized by susceptibility.

When these observations are brought into line with cytological data it is seen that in *Avena*, as in *Triticum*, immunity to parasitic fungi is most strongly in evidence in the species with low chromosome numbers, for these are as follows :—

A. strigosa . .	$2n = 14$
A. brevis . .	$2n = 14$
A. barbata . .	$2n = 28$
A. fatua . .	$2n = 42$
A. sativa . .	$2n = 42$
A. Ludoviciana .	$2n = 42$
A. sterilis . .	$2n = 42$

The obvious line of approach in the effort to obtain greater resistance in cultivated oats would be through hybrids of *A. strigosa* with suitable forms of *A. sativa* and *A. sterilis*, but up to the present it has not been recorded that anyone has been successful in securing a single hybridized grain of these two species. Failing this, the next line of approach appears to be through hybrids of the tetraploid *A. barbata* and *A. sativa* and *A. sterilis*.

Ivanov (1930) gives an account of certain crosses of tetraploid oat forms among themselves and with the hexaploid forms *A. sativa* L., *A. nuda* L. var. *inermis*, Korn *A. Ludoviciana* and *A. sterilis* V.

In a cross of *A. barbata* $\times$ *A. sativa* 25 grains were obtained ; they were all well developed and germinated and grew almost as vigorously as *A. sativa* itself. From these facts Ivanov concludes that high germinating power is dominant. Excepting *A. barbata* $\times$ *A. sterilis* most crosses behaved similarly.

The F_1 plants of tetraploid $\times$ hexaploid oats have a low degree of fertility, but too much reliance must not be placed on an

individual observation in this respect, as under some circumstances, such as unfavourable weather at flowering time, races of most if not all species show a strong tendency to infertility.

The F_1 of *A. Brauni* (spp. of *A. Abyssinica*) × a hexaploid was almost entirely sterile, which indicates that this particular form is farther removed from the hexaploid forms than is *A. barbata.*

It is both interesting and important to note from Ivanov's studies that no gene has yet been found in *A. barbata* which is not homologous with one in hexaploid species. This is the more striking as *A. Brauni* proved to be lacking in certain genes found *A. barbata.*

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CHAPTER IV

FLAX (*LINUM USITATISSIMUM* L.)

This crop is valued for two products—its seed, linseed, and the fibre of the stem, which, after separation from the other plant tissues, is spun into thread and utilized in the manufacture of linen goods.

Linseed is valued mainly for the oil it contains, which varies with the variety and to a less extent with the geographical position in which the crop is grown from 30 to 40 per cent. of the weight of the seed, the higher figure being associated most commonly with Indian flaxes (Ivanov, 1926).

The flax plant (*Linum usitatissimum* L.) is a slender, branching annual, from a few inches to 3 or 4 feet high, with small linear leaves, white or blue flowers, arranged in a many-flowered terminal panicle. The seeds, usually ten in number, are contained in a five-chambered capsule, each chamber having a false division and containing two seeds. The seeds may be brown, fawn and ivory-coloured, and vary in weight from 5 to 12 grms. per 1,000 seeds.

The flaxes cultivated for fibre and seed, respectively, exhibit striking morphological and physiological differences. Thus, true seed flaxes are many-stalked, the stalks or branches arising from near the surface of the soil, and frequently in time producing secondary branches.

The flaxes that are used for fibre production are characterized by long, slender, single stems, with little or no branching at the base, and with relatively few and fine terminal branches forming the inflorescence; they are distinguished also by a short period of growth.

Vavilov (1926) considers that the centre of diversity of the small-seeded group of races grown for fibre and for seed is located in south-western Asia. The largest area of fibre flaxes is the north

of European Asia, and he maintains that the spread of forms towards the south and the north has occurred in strict relation to the length of the vegetative period. The north is thus characterized by early races with long, unbranched stalks, whilst late, short, multi-branched forms, cultivated almost entirely for the seed, are peculiar to the south.

For many years India produced the bulk of the world supply of linseed, but in recent times other countries, more particularly Argentina and the United States, have grown flax seed in rapidly increasing quantities.

The indigenous Indian forms are cultivated entirely for the production of linseed. An examination of the crop in that country has resulted in a classification into 121 elementary species under twenty-six varieties. Two well-marked ecological types demand special consideration here, since to a large extent the economic improvement of the crop rests on the possibility of obtaining a combination of the desirable features of the two types. One of these is known as the Peninsular type from the fact that it is grown south of the line of the Ganges and the Jumna, and to distinguish it from the other type grown on the Gangetic alluvium.

When cultivated at Pusa the Peninsular types grow rapidly at first, and the early formed leaves are large, but the plants lack vegetative vigour, and branching is sparse. Later, the stems become weak and at flowering time are sprawling, in marked contrast to the vigorous, erect types of the Gangetic alluvium. It is noteworthy that the feeble growth of the Peninsular forms is associated with very deep root development, and that secondary roots are not developed until the tap-root has penetrated some distance into the soil. All the Peninsular types form large seeds, rich in oil.

The Alluvium types, on the other hand, grow relatively slowly at first, and are much branched, the stems being strong and rarely procumbent. The tap-root does not penetrate deeply, and secondary roots are abundant and arise from the tap-root at a short distance from the surface of the soil. They produce an abundance of seed which, however, is small and generally poorer in oil than the Peninsular types (Howard and Rahman, 1924).

Howard and Rahman point out how well suited the two different root systems are to the soil and environmental conditions of the areas in which they are cultivated. Thus, in the case of the Peninsular types the length of the period of growth is short, and soil moisture may be a limiting factor of development. The deep-rooted plants, under these circumstances, are not dependant for moisture on surface supplies, since they can readily penetrate to the lower layers of soil for their requirements. On the alluvium, on the other hand, where there is a constant rise of moisture from vast underground supplies, there are ample supplies of moisture available in the surface layers, and there is accordingly no necessity for extensive tap-root development.

Apart from this marked adaptation of the root system of the plant to its particular environment, only one other morphological character appears to influence the yield of seed, and in consequence the economic value of a type, and that is the faculty of branching. This is greatly affected by the fertility of the soil and other soil conditions, but it is nevertheless fundamentally an inherited varietal character.

The authors referred to show that in the case of Type 12, by the use of manures and the adoption of suitable means of aerating the soil, the average number of branches per plant increased from 6·4 in the control to a maximum of 12·1 ; the yield of grain per 100 plants increased also from 415 grms. in the control to 889 grms.

The basis of the economic valuation of Indian linseed is naturally the quantity of oil present in the seed. Commercially a preference exists in favour of pale-seeded varieties with large seed. It is possible, however, that it is the size of the seed rather than its colour that determines the richness in oil content, especially as in this case most yellowish coloured seeds are large; but, as will be observed from the table on p. 93, some large but brown seeds show a high oil content.

As the value of a linseed is of necessity determined by the quantity of oil present in the seed, and as high oil content is closely correlated with large seed, it may be possible to improve the alluvium types by crossing them with those of the Peninsular.

OIL CONTENT AND SIZE OF SEED

Type	Size and colour of seed	Percentage of oil (ether extract)	Mean
1	Bold, yellow	41·85	42·15
2		42·69	
3		41·93	
6	Bold, fawn	43·95	44·01
7		43·31	
80		44·76	
84	Bold, brown	42·32	43·81
103		44·36	
68	Medium brown	38·91	39·15
72		39·38	
12	Small brown	36·18	37·51
19		37·20	
20		40·07	
28		35·12	
29		37·80	
32		37·19	
121		39·00	

Experiments of this character are in an advanced stage and the publication of the results is awaited with interest.

In the meantime several selections made on the basis of yield and oil content have been introduced into the Central Provinces on the one hand, and in the Gangetic area on the other. Two types—No. 12 and No. 121, the former a white, and the latter a purple-flowered kind, have been shown to exceed the local type in yield by about 40 to 50 per cent. Type No. 121, in addition, appears to possess a high degree of resistance to Linseed wilt (*Fusarium lini*).

In 1925, a variant, subsequently grown under the number 124, appeared in Type No. 12, to which it was similar in vegetative and floral characters, but possessed white seed, which on analysis gave 3 per cent. more oil than the parent type. In yield of seed the new type was not equal to Type 121, but not inferior to Type 12. As the progeny of the variant bred true in subsequent generations it is unlikely that it was the product of a natural cross-fertilization.

The cultivation of No. 124 was continued in 1927 and 1928 and the oil percentages of the three types grown under comparable conditions in 1926, 1927 and 1928 are as follows (Scientific Reports of the Agricultural Research Institute, Pusa, 1925 *et seq.*) :—

Linseed type Nos.	Percentage of oil		
	1928	1927	1926
12	37·96	39·39	38·94
121	42·32	41·07	41·77
124	42·65	40·91	42·05

The flax plant has been used as a source of fibre for textile manufacture from early times, and the Egyptians, for instance, used linen fabrics extensively for domestic purposes.

The material obtained from the flax plant for the manufacture of linen is the bast, the bundles of which extend round the inside of the stem in a continuous or almost continuous ring immediately within the thin layer of cortex. The separation of the bast from the other tissues of the stem is effected by first dissolving the pectinous substances binding the fibres themselves together, and to the other tissue, and when this is accomplished further separation is effected mechanically. The first process, or retting, is accomplished by submerging the plant in water for a period of from a week to ten days. The changes then brought about are the result of the activities of aerobic bacteria in the early, and of anaerobic bacteria in the later stages. The process is completed when the cortical layers are dissolved away, and the fibre separates readily from the medulla or pith. At this stage the retted flax is removed from the water and dried, usually by spreading it in thin layers on grass. The final separation of the fibre and the pith is performed on the dried material by means of rapidly driven beaters, which remove the pith, leaving nothing but the pure scutched fibre, and it is in this form that the flax passes from the farmers' into the spinners' hands, and after various processes of cleaning, etc., is spun into thread and then woven into linen fabrics.

The commercial valuation of flax immediately before spinning

is necessarily highly technical for it involves the fineness of the fibres, their colour, length and strength. To the grower the value of the crop is determined not only by the price he obtains for the scutched flax, but by the quantity of the scutched fibre he can produce per acre, and it is by a correct balance between yield and quality that the plant breeder hopes to arrive at an accurate measure of the most desirable lines to propagate and distribute.

Some of the essential morphological differences of the fibre as distinct from the seed flaxes have been outlined above; they are well marked and the separation of the two kinds on this basis consequently offers no particular difficulty. But in the division of the fibre flaxes themselves no generally accepted basis of selection has been arrived at yet, although the problem has been attacked from various angles. Thus, in the Transactions of the Conference of Flax and Hemp Breeders, Leningrad, 1929, the following views are presented: Diakonov expresses the opinion that selection should be based on morphological characters, and after making an initial selection of strictly one-stemmed and one-capsuled plants, he utilizes the diameter of the stem at the middle point of its length as the next character for selection. He finds a considerable correlation between thickness of stem and the percentage of long fibre, between thickness of the stem and length of the inflorescence and average number of capsules, and between length of the stem and average number of capsules. The observations made on the length of the inflorescence lead to the view that this is a critical character.

The views expressed by N. D. Matveiev are in direct opposition to those just stated; this investigator regards breeding on the basis of indirect characters as unreliable, as the characters of quantitative morphology exhibit great variation, and advocates selection based on fibre characters as an essential initial operation.

The basis of the procedure at the Moscow Plant Breeding Station, which Matveiev represents, consists of growing flax selections under comparable conditions, and then determining the quantity of fibre directly by a standard method. As a result of the work at this Station the following are regarded as heritable characters; height of plant, technical length of the stem, per-

centage of fibre, percentage of the technical part, percentage of seed, relation of the length of the stem (excluding the inflorescence) to its diameter at a midway point in its total length, weight of the technical part, and weight of the fibre. Less well inherited are the total weight, the diameter, the number of capsules, and the number of seeds.

Matveiev also showed that the results obtained from tests conducted under field conditions agreed with those obtained in earlier cultivations. An additional test of two pure lines differing markedly in fibre content is significant; in this case comparisons of the fibre content of the two lines grown at four rates of thickness on eight different types of soil were made. In both lines there was a marked constancy in the difference of fibre in almost all the variants, but on fertile soils the fibre content of the two lines became equal.

Of all the flaxes tested at the Moscow Station one, No. 8063, has proved consistently the best.

S. J. Shimanovicz, of the Section of Genetics and Plant Breeding, carried out investigations with a view to testing the value of the correlation method of flax breeding, and at the same time of relating it to the amount and quality of the fibre. In this case twenty-two pure lines have been studied on the basis of the following characters:—

(1) Total height.

(2) Length of unbranched stem.

(3) Thickness of the stem at the base.

(4) Thickness of the stem midway of the total length.

(5) The tapering off, *i.e.* the difference between the character of the stem at the base and at midway of the total height.

(6) The relation of the length of unbranched stem and its thickness at the mid-point.

(7) The number of capsules.

The investigations show that the least varying characters are: (*a*) the total height of the plants, and (*b*) the length of unbranched stem. All other characters vary considerably, maximum variation being shown by the number of capsules.

When the biometrical results and the technological analysis

are viewed together the conclusion drawn is that both height of the plant, *i.e.* the total height, and the length of the inflorescence are connected with the quality of the fibre to a considerable degree, but not always with its quantity.

An important and reliable relation is the negative one existing between the quality of the fibre and the number of capsules.

Another means of determining the value of various lines in breeding is that described by O. P. Kurdumova and V. E. Pissarev, who apply the anatomical method, and from cross sections of the stem determine the following values :—

(1) The area of the cross-section.

(2) The area occupied by the bast bundles.

(3) The percentage of fibre (*i.e.* the percentage of the area under bast fibres to the general area of the section without the medulla).

(4) The fibre index.

(5) The thickness of fibre.

(6) The general diameter of the section.

(7) The number of bast bundles in the whole section.

(8) The number of elemental fibres in the bundles, and in the whole section.

Kurdunova and Pissarev state that each pure line tested affords a strictly individual picture with regard to the configuration of the bast bundles and their arrangement, as well as to the structure of the xylem.

The data from anatomical and technological analyses afford a definite parallelism of value.

In view of the complexity of the interaction of the various features involved in what for fibre purposes may be termed a good flax plant and of the final determination of commercial value on extremely fine quantitative and qualitative points necessitating expert evaluation, the improvement of the crop by breeding has not in the past been, and is not yet, an easy problem. All the various standards of comparison used by Russian and other European plant breeders generally point, however, to the desirability of selecting initially on the basis of long, fine, unbranched stems with a small number of capsules. Technological analysis in some form appears to be a necessary

amplification in all cases, since it will enable a discrimination to be made between various qualities of fibres, and thereby obviate errors that might arise by placing too high a value on the quantity of fibre alone.

Previous to the Great War, the supply of flax seed used in Northern Ireland, where British cultivation of this crop is localized, was entirely Continental, since the crop when grown for fibre is pulled before the seeds are fully ripe. Large portions of the necessary supplies were Russian, obtained direct from Riga and Pernau, and some, which were Russian in ultimate origin, from Holland. Conditions during and subsequent to the war necessitated the organization of home supplies of seed, and brought in its train the whole problem of the nature of inheritance of the agronomic and technical attributes which characterize the desirable flax plant.

Before the urgency of the question had reached its present dimensions, attempts to raise improved strains, and to stimulate interest in the subject were made by a flax grower, Mr. J. W. Stewart, at Coleraine. He was successful in securing the active interest of the Irish Department of Agriculture, who commenced single plant selections in 1910, and ultimately propagated two lines, No. 3 and No. 5, on a field scale. In general uniformity of growth both these lines were decidedly superior to crops raised from supplies of the ordinary commercial seed then available (Hunter, 1915). About 1919 work of a similar nature was started by the Linen Research Association at Lambeg, Belfast, and a line, selected in 1911 and denominated "J.W.S." (in honour of the pioneer work of Mr. Stewart), was established and distributed. This line proved superior to both of the earlier lines, Nos. 3 and 5, and to the ordinary commercial varieties in general use, and was grown extensively in Northern Ireland for a number of years.

From the results of a series of comparative trials conducted in the period 1921–27 inclusive (but omitting 1922) the J.W.S. was ascertained to yield 34 per cent. more scutched flax per acre than commercial sorts. The quality of the flax was also superior, and the monetary return per acre of J.W.S. exceeded that of the commercial sorts by 42 per cent.

Davin and Searle (1925) have studied the correlations of various measurements of the flax plant, made over a period of four years. They found that flower colour, length of the unbranched part of the stem, the percentage of fibre, and the relative earliness of flowering are all strongly inherited characters, and that the same is probably true of the number of seeds in the capsule. The percentage of fibre in this case is the area of fibre as a percentage of the area of the stem in a cross-section through the middle of the stem. It is noted, however, that no definite correlation was found between variations in percentage of fibre and any inherited external characteristics of the plant.

From the examination of a very large number of cross-sections of plants it was found that the fibre in the flax stem may be divided into approximately thirty bundles. These may, or may not be separated from one another, but the existence of a great many intermediate arrangements makes it impossible to say whether the arrangement of the bundles constitutes a genetic character. It was shown, however, that differences in the percentage of fibre do not depend on the spacing of the bundles at greater distances circumferentially, but on a reduction of their radial dimensions. Stems with high percentages of fibre have more rounded bundles. It was also found that the longer stems generally have the more numerous, and, in cross-sections, smaller fibres, irrespective of the thickness of the stem. "From this it follows that the isolation of tall, high-percentage varieties of flax brings with it also a rounding and compacting of the bundles. Such bundles are composed of a relatively large number of small fibres in comparison with the shorter varieties of flax of the same average thickness of stem, these latter having fibres which are fewer in number but larger in size.

"From the practical point of view the two most important facts that have come to light appear to be the inheritance of variations in percentage of fibre and the relationship between the number and size of the ultimate fibres and the length of the stem."

As pointed out above the value of a particular flax to the grower is determined by the yield and quality of the fibre it

produces. In view of existing knowledge the latter feature is not readily defined, but Davin and Searle point out that "it appears desirable to have fine individual fibres with a small lumen and to have well-defined bundles which are regular in shape and uniformly distributed around the stem." For this reason these investigators have determined the number of individual fibres per square millimetre of cross-section of the stem which they term the "fibre index." They state that a high percentage of fibre with a high fibre index is obviously more desirable than one with a low fibre index, as the latter will probably have individuals which are either large in proportion to the stem size, or are of the large cell-cavity type. The fibre index is most useful, therefore, in determining which stems with a high percentage of fibre shall be selected for further propagation.

Proceeding by means of selection based on the estimation of the percentage and index number of fibre, the Linen Industry Research Association have raised the following lines from lots of commercial seed of various origins as follows :—

Pioneer (Liral No. 1) ex-Pskoff seed; Beatall (Liral No. 2), ex-Dedoviezy seed; Monarch (Liral No. 3), ex-Dutch seed; Crown (Liral No. 4), ex-Dutch seed; Purple (Liral No. 6), a sport from Vologda seed; Suffolk (Liral No. 8), ex-Riga seed; Dominion (Liral No. 9), ex-Riga seed.

Two further very promising new lines, Stormont Gossamer and Stormont Cirrus, have been selected by W. J. Megaw of the Ministry of Agriculture of Northern Ireland; in this case the selection was made entirely on morphological characters (Megaw, 1929).

Small quantities of some of these recently obtained varieties have already appeared on the market, but for the most part they are as yet in process of propagation to bulk.

Some of the more promising types, however, were included in the Northern Ireland large-scale flax variety trials of 1930 and 1931, and the results from these tests afford a fairly reliable measure of the progress made. In the two seasons, trials at eleven centres have included Commercial Seed, J.W.S., Stormont Cirrus, Monarch, Crown and Stormont

Gossamer, and the following comparative figures are available :—[1]

	Commercial	J.W.S.	Stormont Cirrus	Monarch	Crown	Stormont Gossamer
Average percentage of Fibre Scutched from Retted Straw.	13·3	14·9	17·4	18·0	17·7	18·3
Average yield of Scutched Fibre. Lbs. per statute acre.	428	564	640	643	639	660
Average value of Scutched Fibre per statute acre, as valued and actually bought by spinners.	208·75 shillings	298 shillings	336·5 shillings	338·25 shillings	341·25 shillings	346·25 shillings

Examination of these figures shows that the amounts of the differences between J.W.S. and commercial varieties, such as Dutch and Pernau, as shown by the 1921–27 trials already quoted, are maintained at almost exactly the same level.

Differences between the members of the more modern group are relatively small, but the group as a whole exhibits a marked superiority to J.W.S. Thus, Stormont Gossamer yields 17 per cent. more scutched fibre than J.W.S., and 54 per cent. more than ordinary commercial sorts. The cash value increase over J.W.S. is proportionate to the yield, and over commercial sorts amounts to 66 per cent.

That all the newer varieties show a definite superiority to commercial varieties in fibre quality is clearly indicated by the increase in cash value being relatively greater than the increase in fibre yield. Differences amongst them, however, tend to be marked by the abnormally low level of prices in general. Such price fluctuations detract from this method of assessing fibre quality and increase the difficulties already mentioned in this connection. In addition to the scutching tests, all the varieties have been successfully spun, but no comparative tests have been made as yet.

[1] Figures kindly supplied by the Ministry of Agriculture, Government of Northern Ireland.

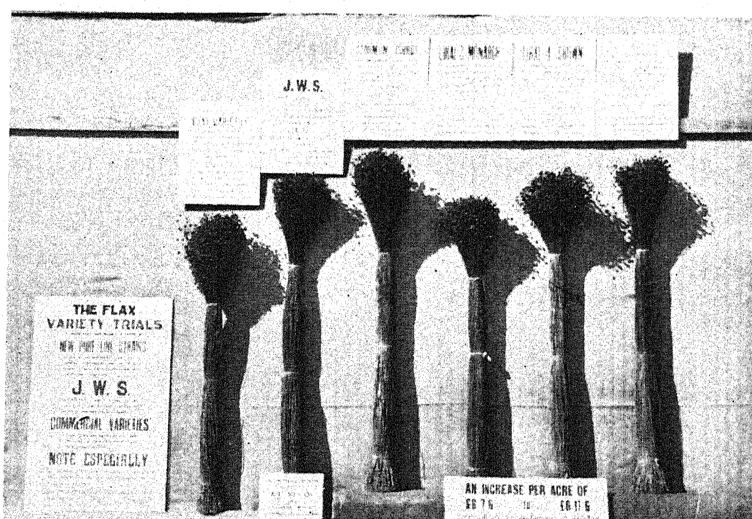
Two other points of interest emerge from these figures, the first relating to the percentage of fibre scutched from the retted straw in each case, which is very low in commercial varieties, slightly higher in J.W.S., and uniformly very high in the new group. This factor certainly has a very direct and important bearing on fibre yield, and from other work already cited may have much to do with fibre quality.

J.W.S. owes its increased yield of fibre over commercial varieties to some extent to an increased percentage fibre content, but in the main to increased height, *i.e.* stem length, but the latest advances are due entirely to increased fibre content, for none of these newest varieties is taller than J.W.S., and some, indeed, are definitely shorter.

The second and remaining point of interest arises from the following consideration: in the case of two of the newer varieties, Crown and Monarch, the claim can be made that the improvement of fibre content has been brought about deliberately, and as the result of continuous selection guided by microscopic examination of the material in cross-section. Stormont Gossamer and Stormont Cirrus, with equally high fibre contents, however, are purely the result of eye selection. Both varieties originated in what appeared to a skilled observer to be "particularly good" plants, and no attempt whatever was made to measure fibre content until sufficient seed was available to make possible the inclusion of the varieties in small-scale tests. Of all the selections from the same source, only four were considered worthy of inclusion in such trials, and the selector's opinion of their relative merits was then amply verified. In this case at least a somewhat empirical procedure has produced a result as valuable as those arrived at by more refined scientific methods. Nevertheless, the morphological characters of the selected plants were identical with those now regarded by the exponents of the more exact scientific methods as the most desirable, since they are correlated with both high quantity and quality of fibre in the plant.

Of the diseases from which flax suffers, Wilt, *Fusarium lini* Bolley, is the most serious, more particularly in the United States,

PLATE V



On the extreme left, sample of flax grown from Commercial seed, followed in order by J.W.S., Stormont Cirrus, Monarch, Crown, Stormont Gossamer. Stormont Gossamer yields about 50 per cent. more scutched fibre than ordinary Commercial seed (*see* pp. 101–2).

(*By courtesy of the Ministry of Agriculture of the Government of Northern Ireland, Belfast.*)

[*To face p.* 102.

where it has resulted in a gradual geographical movement of the crop.

Broekema made some of the earliest observations on the disease and noted that in heavily infested crops some plants remained perfectly healthy. Bolley (1901, 1903) described the causative fungus, and, like Broekema, noted the existence of perfectly healthy plants in crops, the majority of the plants of which were severely damaged. As *Fusarium lini* is capable of existence in the soil as a saprophyte for indefinite periods, it is questionable whether the temporary suspension of the cultivation of flax on "flax sick" soil is a practical solution of the trouble.

The applied value of Bolley's work was undoubtedly the selection, propagation and distribution of Wilt-resistant lines, a preventive measure that has been adopted generally in flax growing districts in the United States.

For a time after the first introduction of resistant types an idea held ground that resistance could be developed in susceptible varieties by association with the disease, and that the maintenance of resistance necessitated the continuance of growth on flax-sick soil, *i.e.* in contact with the pathogene, or, in other words, a Wilt-resistant strain loses its resistance when grown on clean soil. More recent work does not substantiate this claim, but it has been shown that Wilt-resistant forms are not present in all varieties, and that the degree of resistance exhibited is only relative, and may be modified by the temperature.

Tisdale (1917) has shown also that resistance and susceptibility are heritable characters determined by multiple factors, and that resistance is dominant in some crosses and recessive in others, according to the particular varieties used. As in the case of other plant parasitical fungi, there is physiological specialization in *Fusarium lini*, but this has not yet produced insuperable difficulties in securing valuable Wilt-resistant forms in different localities.

A further disease from which flax suffers is Rust, *Melampsora Lini* var. *liniperda* (Pers.), to which both seed and fibre varieties are susceptible. The effect of the disease in the case of the former is to reduce the yield of seed—in some cases by as much as 10

per cent.—whilst in the case of the latter severe attacks may render the crop worthless for fibre production.

Some of the varieties, such as Winona, a seed flax selected from Blue Dutch Minn. 175 by the Plant Breeding Department of the University of Minnesota, which are resistant to Wilt are highly susceptible to Rust; on the other hand, other varieties that are highly Wilt-resistant, as an Argentine selection (used in certain experiments now to be described), in common with certain other varieties, are Rust immune.

Henry (1930) has described a series of investigations carried out with a view to testing the possibility of securing both seed and fibre varieties possessing resistance to both Wilt and Rust. In his experiments he used an Argentine selection, Ottawa 770 B, and Bombay as Rust-immune parents, all of which had been thoroughly tested with different collections of Flax Rust and found to remain immune.

Argentine selection, which was selected from a commercial stock of Argentine flax at Minnesota Agricultural Station, is a large, brown-seeded, late-maturing type of medium height with large blue flowers. The stems are short, coarse and abundantly branched. In addition to being Rust-resistant, Argentine selection is highly Wilt-resistant.

Ottawa 770 B is a yellow-seeded variety with small white flowers. It is taller than Argentine, but neither tall enough nor fine enough for fibre production.

Bombay is a brown-seeded variety with blue flowers. It is short and early-maturing.

The susceptible parents used were Saginaw and Winona; Saginaw is a tall fibre variety with small blue flowers, and small brown seeds. Two other varieties similar to Winona were also used as parents, namely, Blue Blossom Dutch and Chippewa, The latter is a Wilt-resistant selection from Primost, Minn. 25. produced by the Minnesota Agricultural Experiment Station.

In all crosses between these immune and susceptible parents, immunity was invariably dominant. Henry expresses the view that many of the selections from the hybrid progenies will prove Wilt-resistant in addition to being Rust-resistant. This is

particularly likely in the case of Argentine selection × Winona, both of which are highly Wilt-resistant. The existence of resistance to both diseases in the case of Argentine selection illustrates the possibility of securing the two qualities in one variety, and the results of Henry's investigations must greatly extend the possibility of securing distinctly more valuable varieties by breeding.

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CHAPTER V

POTATO (*SOLANUM TUBEROSUM* L.)

THE advent of the potato to Europe took place about the close of the sixteenth century. That it was brought to the Eastern Hemisphere from the Western is undoubted, but the method of transmission, and the exact locality from which it was first procured are still matters for a good deal of legitimate speculation. Two contemporaneous writers, however, have described the new introduction as they actually knew it. One, Clusius (" Rariorum Plantarum Historia," 1601) states that the tuber which came into his possession was long and had a reddish-purple skin ; the other, Gerard (" Herbal," 1597) describes a tuber that was round and white-skinned, and adds that he received his specimen from Virginia, which is not at all unlikely. It is hoped to show later that it is highly probable the potato was cultivated in parts of South America—in Chili, and more particularly on the Peru-Bolivian Plateau, thousands of years before Columbus discovered America. Its spread from one or other or both of these, which may be considered the original centres of origin, to North America is a legitimate conception and is, moreover, one that has been arrived at independently by several authorities. Prescott (1860), for instance, quotes Malte-Brun, Book 86, as follows :—" The potato found by the early discoverers in Chili, Peru, New Granada, and all along the Cordilleras of South America, was unknown in Mexico—an additional proof of the entire ignorance in which the respective natives of the two continents remained to one another. M. de Humboldt, who has bestowed much attention in his early history of this vegetable, which has exerted so important an influence on European society, supposes that the cultivation of it in Virginia, where it was known to the early planters, must have been originally derived from the Southern Spanish colonies.

Essai politique, tome ii., p. 462." Juzepczuk and Bukasov (1929), basing their views on entirely different evidence, also came to the conclusion that "There are indications that the potato was unknown in Mexico at the time of its discovery by Europeans."

The potato forms originally introduced to Europe were both self-fertile, and also fertile when crossed together, and from these two sorts many of, if not all, the varieties in existence in Europe, at least up to 1850, were obtained.

As is somewhat natural, there is no record of the occasion on which the first attempt was made to propagate the potato from true seed, but there is abundant evidence that this mode of raising new varieties was widely known and practised about the beginning of the nineteenth century. Lindley, for instance, communicated the results of tests made with twenty seedlings raised by Thomas Knight to the Horticultural Society of London in 1831, and Lawson states also: "That new varieties may be produced by seed *ad infinitum* is well known." MacKenzie, writing "On the cultivation of the potato" in 1832, remarks that: "If a farmer cannot find a potato adapted for the soil of his farm, he has nothing to do but to begin to raise new varieties from seed, and to go on until he obtains a variety possessing the desired qualities." This, in the light of the present-day experience of the complexity of the issues involved in raising varieties which will meet all demands of grower and consumer, seems a counsel of perfection. Nevertheless Paterson's "Victoria" affords a striking example of the possibility of the success that may be achieved by such efforts.

By growing different varieties in close proximity, or in later times by actually artificially cross-pollinating the flowers of different varieties, the numbers of potato forms were continually increased. But, with the progress of time, the requirements of the farmer and of the consumer became gradually more clearly defined, and consequently, the more pressing objectives in selection. For the farmer high yield and resistance to Blight, and later, other diseases, were regarded as the minima desiderata, whilst for the consumer the shape, the colour and flavour of the flesh, and the cooking properties of the tuber were brought under survey. Thus, large tubers of ungainly shapes, deep eyes and prominent eyebrows,

which were the characteristics of the earlier sorts, were discarded in favour of those of more regular size and with shallow eyes; varieties exhibiting hollow centres ceased to be tolerated, yellow-fleshed forms were replaced largely by those with a white flesh, and potatoes which blacken on cooking were gradually eliminated.

In 1845, an epidemic of potato Blight (*Phytophthora infestans*) spread over Europe with most disastrous effects to the crop, one half at least of which was destroyed. The disease re-appeared in Ireland in 1846, when nine-tenths of the crop were lost. A decimating visitation of this magnitude gave an entirely new direction to the production of potato varieties and, as the objective is yet unattained, one that is still pursued.

"Curl" in potatoes was certainly well known a hundred years before this time and possibly much longer; economically its effects were serious, but those of Blight proved infinitely more so, and led to an immediate and insistent demand for resistant varieties.

Amongst the early efforts to secure resistant varieties, the most notable were those made by W. Paterson of Dundee (1871). In the course of his avocation as a fruit and vegetable grower, Paterson became impressed with the tendency to what he termed "degeneration" in the potato crop, and with the large losses arising from attacks of Blight. There is an element of doubt in Paterson's account of his experiments as to whether by "degeneration" he meant the liability to attacks of Blight only, or whether the gradual weakening in constitution that he noticed might not now, in the light of present-day knowledge, be attributed to virus infection.

It is very probable that he had in mind a single effect arising from two causes, the one Blight, which, however, is chiefly wind and water borne and epidemic in its incidence, and Leaf Curl or some other manifestation of virus disease which is transmitted from diseased to clean plants, primarily by insects. When once plants are attacked by virus their course of degeneration is rapid, for the disease is carried in the tubers and its effects are cumulative. There is a connection, moreover, between virus infection and resistance to Blight which will be discussed later.

After various tentative but wholly unsuccessful attempts to secure resistance to Blight by different cultural methods, Paterson was finally led to carry out the idea he had long held to be the only means of securing improvement, namely, that of raising varieties from the seeds contained in the apples of vigorous and healthy tubers, as we have seen a common practice amongst gardeners and other small cultivators, in addition to seedsmen, in Scotland at that time. This presented immediate difficulties in so far as the varieties in general cultivation in the British Isles were concerned, since most of them had ceased to produce the normal potato fruit. For this reason Paterson's collection of varieties was augmented by supplies from England, the Cape of Good Hope, Australia, America and Calcutta. These were grown in close proximity on carefully chosen soil, the fruits resulting from the various lots were collected, and the seeds sown in due course. The most healthy seedlings obtained therefrom were picked out, and the resulting tubers kept separate and grown in the next and succeeding years until a sufficient quantity was raised to appraise both resistance to disease and other desirable characters. One of the most successful cultures, which was named Victoria, was introduced about 1860.

Paterson's account of his experiments does not leave us at all clear as to the exact parentage of Victoria. The potato plant is largely self-fertile, but it can also be fertilized with pollen from plants of other varieties, and as Paterson grew his many sorts in close proximity, Victoria and others were probably the results of cross-fertilizations. But the potato plant is normally propagated vegetatively and any variety, unless of definitely known origin, may be heterozygous in genetic constitution, and a very mixed progeny will be produced on merely selfing. It was from just such progenies that most of the new varieties were raised in the early part of the nineteenth century. Bearing in mind the nature of the two earliest described tubers, namely, those of Clusius and Gerard, one long and coloured, and the other round and white, the heterozygosity of later generations can be accounted for.

About 1850 an important advance was made by Goodrich by the importation into the United States of an indigenous Chilian

variety which he called Rough Purple Chili. By self-fertilizations Goodrich obtained Garnet Chili, Early Rose and Beauty of Hebron from this variety, all of which in some form or other were introduced into England, and in many cases crossed with Paterson's Victoria.

In the last fifty years very large numbers of varieties of potatoes have been raised and introduced into cultivation. The parentage in many cases is unknown, for the new varieties originated as seedlings of a variety grown in contiguity with other varieties, and hence, probably, the result of cross-fertilizations. Where records have been kept, however, the dominant influence of Paterson's Victoria, and in a less measure of Early Rose, is clearly evident. So diversified has the character of cultivated forms become that distinctly early varieties, varieties of a later habit, and late varieties are available, combined with immunity to Wart disease and, in cases, with degrees of resistance to Blight and virus diseases. The varieties now available are also differentiated on the basis of their yield, and suitability to certain soils and climatic conditions, on their cooking qualities, flavour and keeping quality, and on their suitability for such specialized purposes as the chip-potato trade.

The problem of raising new varieties of potatoes sexually presents difficulties by reason of two or three conditions of the flower: in many varieties, for instance, the flower fails to open, and becomes detached from the plant at an early period of its existence; in others the flower opens, but separates from the plant almost immediately. Flowers of both such classes, from the very small chance of success that they offer of raising seed, are necessarily undesirable as parents. Moreover, the pollen of the potato does not ripen fully until some time after the flower is fully open, and flowers which fail to open, or open only partially, are useless as pollen parents.

Another feature involving serious disability in this connection is that in some varieties which flower freely the anthers contain no pollen. In these cases, of which Up-to-Date is an example, the flower is readily fertilized and sets seeds when pollen of any other variety is introduced. Sterility is thus confined to the male side

and Salaman (1910) has shown that this condition is a dominant character.

The desirability of obtaining varieties of potatoes that are resistant to Blight still exists, but the introduction of the practice of spraying the haulms with compounds of copper and lime or soda, in either a liquid or dry state, has greatly reduced the risks attending the cultivation of the crop. According to Pethybridge (1921) the first potato spraying trials were made in France by Joult in 1886, and more precise trials by Prillieux in 1888. The essentials of success in the use of these prophylactic measures are the complete covering of the leaf, especially the underside, with the spray or powder, which acts as a fungicide, and, provided the disease has not already infected the leaf, prevents its entrance through the stomata.

The two fungicides known as Bordeaux and Burgundy mixtures, the one prepared from copper sulphate and lime and the other from copper sulphate and soda, have proved most effective, and in areas commonly subject to Blight spraying is now regarded as a regular routine operation.

The general consensus of experience of breeders is that there is no European and North American variety definitely immune to Blight, although there are, and have been, varieties which display a high degree of resistance to it. A most disconcerting feature of such varieties is that they lose this resistance in the course of a relatively few years. Recent investigations have established a close connection between infection of the potato plant by virus diseases and its resistance to Blight, and this phenomenon will be discussed when dealing with virus diseases.

As a result of some investigations on resistance to *Phytophthora* in the potato, Müller (1925, 1928, 1930) points out that certain varieties that are commonly regarded as highly resistant are late-ripening types, and in virtue of this character they escape the period of maximum *Phytophthora* attack ; thus, they are not truly resistant in the pathological sense, but rather merely disease-escaping, and when artificially infected they prove susceptible. In this respect they may be likened to certain varieties of wheat and oats which are known to escape attacks of Rust, or at least to

suffer therefrom in a greatly reduced degree, by reason of their earliness.

In the case of a series of hybrids denominated the *W* races, obtained from crosses of South American and commonly cultivated forms, there was found to be true immunity. Although these hybrids were late in ripening the immunity to *Phytophthora* was not a resultant of this character, since when grown in disease-free soil in comparison with susceptible varieties with the same period of maturation they retained their immunity. In infected soil the *W* races were affected only when nearing the termination of the growth period.

The study of the manner of inheritance of resistance showed several complications, in some cases arising from the heterozygous character of the parents, and from the fact that resistance involves more than one genetical factor. Müller concludes from his observations that there are at least six types of segregation of resistance, and that resistance is not closely linked with any of the important commercial attributes of the crop. The possibility of ultimately obtaining new resistant varieties from the *W* races is increased by the fact that up to the present no evidence has been forthcoming of the physiological differentiation of *Phytophthora.* Moreover, as the *W* races are the product of a hybridization of which one parent may have possessed resistance of a genetical rather than a physiological nature, the chances of securing resistance which is independent of limitations imposed by the length of growth period are considerably enhanced. But, until the exact nature of the resistance is determined, the breeder cannot evade the possibility of the gradual loss of resistance which has been the fate of so many initially promising varieties.

In the United States, Reddick (1929) found that the Japanese variety Ekishirazu remained highly resistant to Blight in a series of trials conducted at Ithaca, New York, during the period 1921–1927. Unfortunately this potato possesses no commercial value in the United States, and it was accordingly crossed with varieties of proved value such as Irish Cobbler, and some unnamed Alsatian forms. From these hybridizations a number of families were obtained which combined the Blight resistance of Ekishirazu and

the desirable economic attributes of the other parents. Leaf Roll, however, has become prevalent in the Blight-resistant families.

Reddick (1930) also attempted to secure crosses with *S. demissum*, which is immune to *Phytophthora infestans*, and *S. tuberosum*, but with little success.

With regard to the occurrence of *Phytophthora infestans* in South America, Abbott (1931) from observations made in Peru in 1928, 1929 and 1930 found that the disease affected neither the wild nor the cultivated species of *Solanum* at elevations above about 9,000 feet. In 1928, a small amount of Blight was found in the Arequipa Valley (8,000 to 9,000 feet). On the other hand, the disease is present and frequently severe along the coast, especially in the vicinity of Lima, where importations of potatoes from Europe and the United States have been frequent in recent years. These facts, Abbott considers, support Reddick's theory that Blight is not indigenous to South America. That the freedom from disease of varieties grown at the higher altitudes is not due to their possession of physiological resistance is demonstrated by their susceptibility when grown in the coastal areas.

Whether the permanent solution of the problem of obtaining resistance to Blight is to be found concomitantly with resistance to or immunity from viruses, is a question awaiting solution. Although a high degree of resistance to Blight has been obtained in different European and North American varieties from time to time, it is nevertheless possible that these forms are too closely alike genetically to enable the breeder to obtain immunity.

In the past, several efforts have been made to obtain hybrids by crossing the cultivated sorts with wild-growing varieties such as *S. commersonii*, *S. Maglia*, but the resulting progeny has displayed such undesirable characters as long stolons, low cropping, and extreme lateness in maturity, that efforts in this direction have been entirely devoid of economic value.

Despite these earlier non-successes, the whole question of utilizing some of the original forms of the potato has been reopened by the results of the botanical explorations carried out by members of an Expedition of the Institute of Applied Botany, Leningrad, in Central and South America, which have greatly amplified our

knowledge of the botanical, ecological and cytological nature of the cultivated and wild-growing potato.

Applying the number and diversity of forms as the criterion of the centres of origin, Juzepczuk and Bukasov (1929) reached the conclusion that the Island of Chiloe and the surrounding islands off the southern coast of Chili is the centre from which the cultivated potato of Europe and North America, *S. tuberosum, sensu stricto*, is derived, and that the second centre is the Peru-Bolivian tableland, where twelve cultivated species were identified. The latter form a polyploid series with 24, 36, 48 and 60 chromosomes. Only one of these, *S. andigenum*, has 48 chromosomes—the number of the ordinary European and American cultivated varieties, and while *S. andigenum* is widely distributed in the whole Andean area, the other species are very localized ; *S. andigenum* is totally absent in Chiloe, and the Chiloe forms are not found in the Andes.

The conception of the Peru-Bolivian plateau as a centre of origin is supported by striking evidences of a Megalithic civilization in that region. This, combined with a wide diversity of cultivated plants found in that particular area, indicates that the potato was only one of many plants brought under domestication and utilized by an early people who were extinct long before Columbus discovered America.

Although on historical and other grounds it is considered that the potato was unknown in Mexico in prehistoric times, there is an exceptionally wide diversity of forms of wild potatoes found there to-day, many of them closely related to *S. tuberosum*. Nevertheless the cultivated form at present in use in Mexico is the Andean form, *S. andigenum*, not *S. tuberosum*.

Of the wild potatoes found in Mexico there are about thirty species, and these again form a polyploid series with 24, 36, 48, 60 and, in the case of one species, *S. demissum*, 72 chromosomes. Included here are *S. commersonii* and *S. Maglia*, and these, according to Rybin's (1930) cytological examination, have 36 chromosomes, which fact probably accounts for the irregular genetic behaviour of crosses between these varieties and the cultivated forms.

The potential value of these investigations for breeding lies

primarily in the diversity of both cultivated and wild-growing forms, in their ecological differences, and in the fact that some of the newly described species in both groups exhibit resistance to *Phytophthora infestans*. *S. andigenum*, for instance, shows some resistance and amongst the wild growing forms, *S. Antipoviszii* ($2n = 48$) and *S. demissum* ($2n = 72$), which cross readily with *S. tuberosum*, are immune to *Phytophthora infestans* and some other diseases.

It is noteworthy, nevertheless, that in both groups forms have been found which are distinctly susceptible to the disease.

About the beginning of the present century wart disease (*Synchytrium endobioticum*), which causes very characteristic excrescences on the tuber and other parts of the potato plant, claimed considerable attention. The fungus responsible for this disease is of a low type which is spread in the soil by spores arising from resting bodies and rendered capable of a certain degree of movement by means of flagella. Once the fungus has penetrated into the superficial cells of the tubers and stems of the plant, the stimulus of infection leads to rapid cell proliferation, producing in time the characteristic irregular, warty outgrowth. The soil becomes re-infested with resting spores from the infected tubers. Tubers suffering from wart disease are entirely unfit for human consumption and undesirable as food for livestock.

Wart disease appears to be most prevalent in wet seasons and in soils that are naturally moist. Fortunately, in this country the spread of Wart disease had no sooner commenced to assume serious proportions than some varieties were found to possess complete immunity to this serious trouble. But many of the most economically desirable sorts of varieties, such as Epicure (Early), Up-to-Date and King Edward Maincrop, were susceptible, and this led to a complete reorientation of schemes of potato improvement.

Salaman and Lesley (1921) have shown that immunity and susceptibility to Wart disease are inherited in the Mendelian manner, and that immunity is a dominant character. The number of factors involved, however, is not the same in all crosses, and the ratios of immune and of susceptible individuals arising in hybrid progenies consequently differ also.

In the case of certain varieties such as Leinster Wonder and Edzell Blue, which have been ascertained to be immune to the disease, selfed-progenies produced a number of susceptible forms. Two immune varieties, Golden Wonder and Leinster Wonder, when crossed, also produced some susceptible forms. These results appear to imply the presence of more than one factor for immunity, and that some varieties may be heterozygous for the particular immunity factor they contain.

Köhler (1925, 1929) has also shown that immunity and susceptibility for this disease are segregating characters.

Up to the present no physiologic forms of the disease have been isolated, but the presence of factors inhibiting immunity has been demonstrated.

Fortunately, no linkage between Wart disease and any other character of the plant has been established, and the problem of securing resistant varieties possessing desirable economic characters is not consequently complicated thereby.

Amongst recent introductions of varieties that are immune to Wart disease the Arran series (MacKelvie)—Arran Crest, Arran Pilot, Arran Banner and Arran Victory—are particularly notable.

The cultivation of the potato, and the raising of new varieties have been profoundly affected in the last ten or fifteen years by the results of studies of a series of pathological diseases grouped under the general head of Virus diseases. The number of cultivated plants that suffer from Virus diseases is a large one, and is unfortunately constantly being increased; it includes both tropical and semi-tropical plants and up to the present the number of Virus diseases that have been described exceeds a hundred. The actual cause of the disease has not been discovered, partly because it has not yet been found possible to culture it on artificial media. In general, virus diseases differ from other plant diseases in so far as they are not localized, but occur in every part of the host, with the possible exception of the seed (Kenneth Smith (b), 1931).

The manifestations of Virus disease on the potato host are very varied: they may be recognized by discolourations and by various distortions, such as rolling, crinkling and puckering of the

leaf, and often by characteristic rings on the leaf. In some types distinct lesions appear on the leaf, and ultimately bring about not only its destruction, but, at times, that of the whole plant; in others again the whole plant is dwarfed.

The effects of Virus diseases in the potato are serious economically since they result in an almost immediate reduction in the yield of tubers, and because the disease may be carried in the tuber; when this happens, as is frequently the case, the effect is rapidly cumulative, and the final result is a complete failure of tubers so infected to reproduce themselves. Much has been, and may still be, done to reduce the probable losses, by rogueing plants exhibiting Virus disease in any form from crops that are intended to be used for "seed," but the early symptoms of the disease are difficult to detect, and the manner of infection renders any procedure of this nature only a partial measure of protection.

In the field, potato viruses have been shown to be disseminated by various groups of insects, particularly Jassidæ and Aphididæ; of the latter the aphis or green fly, *Myzus persicæ*, is associated with no less than fourteen viruses. Artificially, virus may be transmitted by grafting, and in some cases by inoculation by a needle (Smith (b), 1931).

The full technique of the manner of virus transmission is too lengthy a subject to be followed in detail here, but some particular aspects, in so far as they affect measures that may be adopted to control the disease, must be mentioned.

It has been shown by Smith ((a), 1931) that certain potato viruses are composite in character, and that potato Mosaic, for instance, consists of two forms, which, for purposes of description, may be denominated x and y. The virus x may be transmitted from an infected to a healthy plant by a needle scratch, but not by aphides; virus y, on the other hand, is transmissible by both methods.

The same investigator found that certain plants are resistant to one or other of the constituent viruses of the complex $x + y$, and actually act as filters to one or other of these constituents. Thus, *Datura stramonium* and *Solanum dulcamara* are resistant to and filter out the virus of y, whilst the garden variety of Petunia is resistant to and filters out the virus x. Smith also showed that

an analysis of the x and y virus complex can be made by taking advantage of the rate of movement of the respective components in the plant.

Another aspect of the problem arises from the fact that some varieties of potatoes can carry but bear no visible outward manifestation of a virus ; Up-to-date, for example, carries Streak, and King Edward is a carrier of a severe form of crinkle. A still further complication arises from the finding that common Solanaceous weeds such as Black Nightshade (*Solanum nigrum*) may also be symptomless carriers of potato viruses, which on occasion may be transmitted to the potato by the aphis *Myzus persicæ*.

Up to the present no case of a Leaf Roll virus carrier has been recorded, but Salaman (1926) considers that Great Scot manifests a certain degree of tolerance to that virus.

Some idea of the economic significance of potato Virus diseases may be gathered from figures given by Smith ((c), 1931), who shows that in one particular series of yield comparisons the return from plants affected with Leaf Roll was 61·5 per cent. less than that obtained from apparently healthy plants.

The most desirable line of approach in combating Virus diseases appears to be in the direction of securing Virus-immune varieties, but unfortunately no varieties answering to this description have been discovered yet. Failing a solution of the problem along these lines some mitigation of the trouble may be secured by developing stocks of seed under conditions of immunity to infection. The difficulties attending such operations are many and very obvious, and the breeder can only hope for more direct possibilities with increased knowledge of the nature, and, possibly, of the origin of viruses themselves. In the meantime it is well known that crops raised in areas of low mean temperature are less infected with green fly aphis than those produced where the normal summer temperature is higher, and the long-established practice of obtaining " seed " from such areas is as fully justified scientifically as it is by long experience. Nevertheless, the value of " seed " still rests on its initial freedom from Virus disease, and not on the length of time it may have been grown in a special area, for apparently no method of cultivation (which may include produc-

tion in a special area), or of manuring will rid a tuber and its vegetative produce of Virus diseases once they are infected with the disease.

The manner of propagating the potato has been alluded to previously; in ordinary agricultural practice this is done vegetatively and by this means some varieties have been maintained in an unaltered condition through a long series of generations. But in the majority of cases the life of a potato variety is short; breeders in the last century seemed agreed that twenty-five years might be regarded as an average length of life, although some indeed held that most varieties would not last longer than fourteen years, and that after such a period they degenerated rapidly, and ultimately passed completely out of cultivation. Nevertheless, in the case of a few varieties, of which Myatt's Ashleaf Kidney is an outstanding example, the life has been much longer, but it must be added that this has not occurred in general cultivation, but only in a few very sharply delimited localities. Since no theoretical reason can be advanced for a general deterioration of this character and extent arising out of the manner of propagation, the underlying causes must be sought in another direction.

Contemporaneous agricultural and horticultural literature from 1750 onwards abounds with references to the losses arising from Curl in the potato crop, and with the various measures adopted to limit its destructive influence. The nature of Curl as described by these writers, and its ultimate effect on the production and productivity of tubers, bears an exact similarity to this disease and its effects as we know them to-day. Furthermore, the results of studies such as those just recapitulated have shown that Curl is one of the group of Virus diseases from which the potato is liable to attack. This evidence of a direct nature is convincing and does not necessitate confirmation, but if such were desirable the reverse phenomenon, that is, the production of plants of a variety with none of the visible manifestations of disease, and possessing its pristine vigour and productivity, should satisfy the most sceptical.

Very suggestive results from investigations of this description

arise from a recent attempt made to rejuvenate the Champion potato in Ireland. This variety was raised by John Nichol, the gardener to the Laird of Ochterlang, Forfarshire. It was produced as a seedling from seed obtained from two white-tubered varieties, one of which may have been Paterson's Victoria (the name of the other was not remembered by the raiser), and one red potato grown in near proximity; the seed so obtained was sown in 1863, and from this the seedling afterwards named Champion was derived. Champion was introduced into Ireland between 1877 and 1880, and thus encountered the severe Blight epidemic of 1879. The high degree of resistance to that disease displayed by the new potato marked it out as a most valuable addition to the varieties then in use—a distinction which was later enhanced by its excellent quality and flavour.

Gradually, however, Champion lost its power of resistance to Blight, and in 1921 Pethybridge (1921), who had made an extensive study of the varietal incidence of Blight in Ireland for a number of years, remarked that, "Nowadays, probably, it would be difficult to find a variety which was more susceptible to Blight."

Champion is resistant to Wart disease, and for that reason, and because it is highly valued for culinary purposes in Ireland, Davidson (1928) attempted to revive the variety there. The initial procedure adopted in this case was a search for individual plants exhibiting freedom from such virus diseases as Mosaic and Curl, and as features for guidance he used, amongst others (*a*) the size of the leaflets, (*b*) flatness of the leaflets, and (*c*) absolute uniformity in the colour of the leaflets. This basis of requirement proved exacting even in Ireland, where Champion is still grown in considerable quantities. When roots answering to this description were finally obtained, their freedom from Mosaic was verified by grafting cores of tubers, and later, of cuttings, from the selected units on to President potato, which exhibits clear symptoms of Mosaic whenever it is present. These findings were further verified by growth trials and inspections in later years. The selected products were planted in Donegal in 1927, in which year Blight was prevalent, but notwithstanding this condition the crop remained green until the third week in October, and withstood the

disease better than varieties such as King Edward, Arran Chief, Kerr's Pink and Arran Victory grown in the proximity.

It was not possible to make comparative yield tests at that time, as the quantity of the rejuvenated stocks was limited and, moreover, it was undesirable to grow them in close proximity to other unselected, and possibly Mosaic-infected stocks, but such weighings as were possible showed the total yield to be approximately $11\frac{1}{2}$ tons per acre, a figure greatly in advance of that obtainable from normal unselected Champion seed.

The production of Virus-free stocks of a variety of old standing exhibiting the high yielding potentiality of its earlier days is not more remarkable than the fact that the variety also recovered the resistance to Blight which it previously possessed. The dependance of resistance to that disease on the absence of virus diseases, and its loss on their advent is paralleled by the loss of resistance to *Puccinia glumarum* in wheat when the plant is attacked by Bunt (*Tilletia caries*). Davidson's investigations for the special reasons mentioned were concerned with Champion only, but his findings may be applicable to other varieties, and if so the necessity for the prosecution of measures that will secure control of virus diseases is emphasized in a striking manner.

In addition to the production of new varieties by self- or cross-fertilization, new forms arise at times by mutations of the bud. Such mutations may affect the colour of the flower, and the colour of the tuber, and may, in some cases, be extended to comprehend changes in the shape of the leaf. The changes appearing under this heading at times involve the loss of a character, either wholly or in part; at other times they partake of the acquisition or intensification of a character.

Of the former types of mutation an example is provided by MacKelvie (1921), who described three types found in Arran Victory—a variety with round tubers, purple skin, white flesh and purple sprouts; the leaves are open, dark green, and rather glossy. Arran Victory is immune to Wart disease, and highly resistant to Blight. The first abnormal tuber was coloured the usual purple over half its length, the other half was free of any colour. This was found in a pit of Arran Victory in 1919, and planted whole in

1920. It produced a plant with the usual foliage characteristics and 41 tubers, 36 of which were of the Arran Victory type and 5 were very small white tubers with purple eyes and a purple spot at the heel end. The 36 normally coloured tubers produced the usual Arran Victory type in 1921, and the 5 parti-coloured gave parti-coloured tubers.

The second aberrant tuber had a pale-pink skin, and dark-purple eyes and heel end. The haulm in 1920 was of the Arran Victory type, and the tubers were pale pink with dark-purple eyes and heel end. Planted in 1921, these tubers reproduced the plant of 1920 in all its characteristics.

The third aberrant tuber was a white-oval with a spot of purple at the base of the sprout, a dark-red or purple sprout, and a spot of purple at the heel end. This tuber when planted in 1920 produced a haulm identical with Arran Victory, and five white tubers with purple eyes and purple spot at root end, and nine entirely white tubers. The five partially coloured tubers produced plants of the ordinary Arran Victory type, and the tubers retained their original character. The other nine tubers produced plants, the haulms of which were alike, but not so tall as those of adjoining plants of Arran Victory; the leaflets were longer, narrower and distinctly lighter green than that variety. In the case of five of the nine plants the tubers produced were all white and varied in shape from oval to round; the remaining four plants gave rounder tubers, most of them white, but in the case of each of the roots four or five of the tubers were marked with a few small purple spots.

So far as information is available the variations detailed above involve only changes of a morphological character. Changes involving morphological and physiological characters concurrently have been recorded by Van Luyk. In this case a plant of the variety Zealand Blue, which exhibited Mosaic in 1911, produced tubers which showed Mosaic again in all but one plant. This one plant grew a stronger haulm, broader and smoother leaves, and its tubers were not round and violet like the Zeeland Blue, but long and dark violet. The plants produced from these tubers (in 1913) were of four types: one type had round white tubers;

a second had hard, violet, long tubers ; a third in no way differed from Zeeland Blue, even to the extent that it exhibited Mosaic, whilst the fourth type (consisting of one plant) was vigorous, with large, broad, smooth leaves and exhibited some resistance to Blight. The tubers of this plant were of three types : one type was the Zeeland Blue ; one was dark violet and long ; and the third pink and long, which in the following year reproduced pink, long tubers, but the plants did not possess resistance to Blight and Mosaic.

The white tubers (of 1913) yielded white tubers in the following year and the plants again were Mosaic-free.

As an illustration of an additive effect the whole-coloured red King Edward may be cited. In this case the red flushing peculiar to the eyes is extended to the whole skin, but this change does not involve either any other morphological or any physiological character.

The problem of vegetative mutations has been studied by Asseyeva (1930), who found that the aerial portions of the plant as well as the tubers may be altered in colour, shape and structure, and that gain and loss mutations occur equally frequently.

The procedure adopted in the investigation of colour mutations affecting the tuber was as follows : the mutating tuber was cut in half about two months before planting, and the eyes of one half removed 1 to 2 mm. deep, the other half remaining untouched and serving as a control. In the spring, the two halves were planted separately. The half from which the eyes were not removed developed into plants which repeated the characteristics of the mutating parent plant, whilst that from which the eyes were removed developed (in 25 to 30 per cent. of cases) into plants unlike the mutating parent plant, but similar to the normal plant from which the latter originated. Thus, in the case of a blue-coloured tuber arising from a normally white tubered variety, half of the blue mutant tuber produced blue tubers again, whereas the half with the eyes removed produced white tubers like the original white-tubered parent.

The explanation Asseyeva offers for this phenomenon is that in the majority of cases the vegetative mutations affect the epidermal

tissues only, all the inner tissues remaining normal, consequently, when the eyes of a mutant tuber are removed entirely, the new buds developing from deeper-lying tissues are unaffected by changes arising in the outer tissues, and give rise to plants which are indistinguishable from normal plants of the variety.

Asseyeva regards mutations of the nature of those just described as periclinal chimeras, and recognizes three types arising from the fact that the cells containing the anthocyanin pigment are located in layers in the periderm which are formed partly of epidermis and partly of sub-epidermis, and these layers can have a different complex of colour factors in chimeric mutants. Consequently, in cases where the epidermis only mutates, the colour of the whole surface of the tuber changes with the exception of small, irregularly scattered patches or the "eyebrows," and these exhibit the normal primary colour. In other words, changes in the epidermal layers affect the whole of the tuber excepting the eyebrows.

The distribution is quite the reverse if the sub-epidermis mutates, and when both layers mutate the colour of the whole surface of the tuber changes, and only very occasional small spots, corresponding to the usual primary colour, are visible.

A close relation is observed between the colour of the tubers and that of the stem, but the pigment in the stem is chiefly situated in the sub-epidermal layer, and changes in stem colour occur only when that layer is affected. If the epidermal layer mutates, then the relation between tuber and stem colour is not maintained. As the sprouts depend for colour on the sub-epidermal tissue, the changes observed in them follow a course similar to that found in the stems and in the tubers.

Mutation of the stem colour in these investigations was found invariably to be connected with that of tuber colour.

In some cases the shape of the corolla changed from the normal wheel-like shape into the star-like form.

Asseyeva found mutations of the leaf to be many and very diverse. Even small changes in the leaf were met with, but they were transmitted constantly in vegetative reproduction, and may thus be regarded as mutations rather than merely modifications. Especial interest attaches to the observations on

"wildings," which are not uncommon in all potato-growing countries. "Wildings" differ from the normal plants by the proliferation of stems, feeble dissection of the leaf, absence of flowering, and by the reduction of the size of the tubers. They usually retain the various features by which they are characterized when reproduced vegetatively, but Asseyeva succeeded in securing a return to the normal form in a few cases by removing the eyes and thereby restricting reproduction to deeper-laid tissue. This indicates that "wildings" also are periclinal chimeras.

Coming to the genetic behaviour of vegetative mutants with periclinal chimeric structure: as the gametes of the plant arise from sub-epidermal layers, the transmission of a mutating character by the true seed can take place only when these layers are affected by the mutation. A mutation of the epidermal layer, on the other hand, is not transmitted by seed, and seedlings of selfed plants exhibiting mutations of this nature produce nothing beyond the characters of the original normal form.

A group of mutants of peculiar character is one in which the tubers are white with large violet or red patches around the eyes, which are dark coloured. This colouring remains constant in vegetative reproductions, but at times almost wholly white tubers with very small speckles around the eyes which are without colour, appear on some plants. Tubers of this description remain constant in vegetative reproduction, but occasionally change to the original form with large spots and dark-coloured eyes.

On "selfing" the original form, three groups of seedlings are obtained, namely, "large-spotted," white with coloured eyes, and entirely white tubers. When the "large-spotted" are crossed with Alma, which has continuously coloured tubers and light eyes, a fourth group is found—the "hidden-spotted." In this a layer of continuous colour covers up the large spots, which consequently stand out in the general coloured background, and the eyes are dark.

The removal of the eyes of the "large-spotted" forms and of the "large-spotted" seedlings gives rise to small, speckled tubers which transmit the small speckledness in subsequent vegetative generations and are not affected by the removal of eyes. But when the

eyes of the "hidden spotted" are removed, an entirely new form called the "spectacle-spotted" is obtained. In this race the general background of the tuber is coloured, but the portions around the eyes are large and sharply outlined, with white spots, and the eyes themselves are light coloured.

The "spectacle-spotted" and the "hidden-spotted" colours are met with frequently in some of the native varieties of South America, and the two types not infrequently interchange in vegetative reproduction. The removal of the eyes in a South American variety, the Uraquayian, transformed the "hidden-spotted" into a "spectacle-spotted" race, but the same operation did not make any noticeable change in the latter.

On self-fertilization, "spectacle-spotted" varieties yield a large number of "spectacle-spotted" seedlings, but not a single "large-spotted" one.

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CHAPTER VI

FORAGE GRASSES

PERENNIAL RYE-GRASS (*LOLIUM PERENNE* L.) and COCKSFOOT (*DUCTYLIS GLOMERATA* L.)

THE value of forage grasses for feeding, whether in the green condition or as hay, is determined primarily by their chemical composition, chiefly in regard to the protein, fibre and ash content. But since the composition of the various organs of a plant varies with their age and, consequently, their stage of development, the feeding value is not absolute but relative to that stage.

The biological functions of the plant may be considered under the headings of those which are denominated vegetative, *i.e.* the development of leaves and stems, and reproductive, or those concerned with the production of seed. As forage grasses are mainly perennial, vegetative development does not cease with the formation of seed, although activity in this direction in any one year is greatly reduced after flowering; in cereals, another important division of *Gramineae*, however, the life of the plant terminates within fairly restricted limits of time, but the extent to which the grain is developed is largely dependent on the character of the weather subsequent to fertilization. The nature of the changes in the chemical composition of the plant as it advances from vegetative to reproductive activity is similar in grasses and cereals, but for the reason stated they are more sharply defined in the latter; nevertheless, for purposes of illustration the sequence of changes occurring in cereals may be summarized briefly as follows: in the British Isles spring-sown barley, for instance, occupies the ground for a period of about 150 to 160 days from the time of sowing until the crop is fully ripe and fit to cut. During the first 100 days, designated the vegetative period, the plant develops leaves and flowering stems. The plant flowers at the conclusion

of about 105 to 110 days' growth, fertilization synchronizing with the appearance of the ear from the leaf sheath, but occasionally being effected whilst the ear is still enclosed in the leaf-sheath. The development of the caryopsis commences immediately fertilization is completed. Subsequently, further vegetative development is very limited, but the weight of the whole plant increases steadily for another twenty days or thereabouts. During the period of grain filling there is a steady increase in the actual amount of nitrogen in the plant, and this is found concurrently with a steady and regular increase in the percentage of dry weight to green weight. But concomitantly with the increase of total nitrogen in the whole plant there is a sharp fall in the percentage of nitrogen and phosphoric acid in the dry matter of the straw, and a rise in the actual amount and in the percentage of nitrogen in the dry matter of the grain. These changes may thus be regarded as the resultants of the translocation of material from the stem and leaves to the rapidly developing grain. But as a period of desiccation sets in about three weeks before the grain is completely ripe, the percentage of fibre found in the straw or stem of the plant shows a substantial increase, the actual changes in this direction depending upon the extent to which transference of material from the straw to the grain has been effected.

During a period corresponding to that just outlined for barley the changes in the chemical composition of grasses are similar to those occurring in that cereal, namely, there is a period of vigorous vegetative development culminating in flowering and the fertilization of the ovary, followed by a further period during which vegetative activity is greatly reduced and material is transferred from the stems and leaves to the seed, and finally, a period of desiccation particularly affecting the flowering stems.

But several circumstances operate to modify the comparison between the two classes of plants in so far as their final utilization is concerned.

The differences in chemical composition between pasture grass and hay concern mainly the protein, fibre and ash. Thus, with increasing age and under the operation of hay-making, which is essentially a process of desiccation, the percentage of protein and

	Crude Protein		True Protein		Fibre		Ash	
	Stem Shoots	Leaf Shoots	Stem Shoots	Leaf Shoots	Stem Shoots	Leaf Shoots	Stem Shoots	Leaf Shoots
Timothy . . .	8·29	10·38	6·94	8·85	26·1	21·7	3·86	5·09
Cocksfoot . . .	8·76	12·32	6·79	10·41	26·2	22·3	4·85	5·79
Meadow Foxtail . .	8·57	13·50	7·66	11·78	26·5	22·8	4·64	5·48
,, Fescue . .	8·38	13·38	6·88	10·88	24·9	21·3	5·62	6·30
Smooth-stalked Meadow Grass . . .	8·25	11·19	7·44	9·69	25·9	23·5	4·19	4·73

Figures taken from " Toxestorp " from Osvald " Undersökningar öfver fodervärdet hos olika gräs från slättervallar på torfjord " in *Svenska Mosskulturföreningens Tidskrift* Ar. 1919, p. 156 (see Stapledon, 1927).

of ash in hay decreases, whilst that of fibre increases. Apart from the question of the stage of growth at which the crop is cut, and the losses of leaves and seeds incidental to the process of haymaking, the feeding value of hay is influenced by the quantities of leaf shoots as distinct from stem shoots present, as will be seen from the table on p. 130.

If the analysis of the component parts of the plant that contribute to the formation of hay is carried a step farther, as in the table on p. 132, the respective value of each class of leaf, and of the stem and inflorescence become evident. The figures which relate to Cocksfoot only show the difference in composition of the various parts of the plant at the beginning and end of flowering.

As the meristematic tissue in the growing portions of a plant is constantly giving rise to new, thin-walled cells completely filled with protoplasm, the reason for the high value of the root leaves (*i.e.* leaves at the base of the plant) which are the youngest, is clearly evident. The gradual denudation of the leaves and stem of protein, and its concurrent accumulation in the inflorescence, is again emphasized. The order of the leaves in richness of protein will also be noticed, the uppermost leaves, being the youngest and consequently possessing the most active meristem, contain the largest quantity of protein, and approximate most closely to the root leaves in this respect.

Before passing to a discussion of the relations of the figures just quoted on the broad question of the possibility of improving grasses by breeding, there remains the consideration of differences in the composition of the species themselves. In this connection figures published by Fagan and Jones (1924) for pasture hay and aftermath show that in the case of the ten species Cocksfoot, Perennial rye-grass, Timothy, Tall oat-grass, Golden oat-grass, Crested Dogstail, Red Fescue, Meadow Fescue, Tall Fescue, Meadow Foxtail, the greatest range of difference in crude protein, true protein, fibre and ash occurs in the hay (see table on p. 133).

The greatest differences in the crude protein, true protein, fibre and ash of pasture and hay occur in the following species :—

$$\text{Crude protein} \begin{cases} \text{Pasture} & 15{\cdot}5 \\ \text{Hay} & 7{\cdot}6 \end{cases} \Big\} \; 7{\cdot}9 \quad \text{Tall oat-grass.}$$

Parts of the Plant	Crude Protein		Pure Protein		Fibre		Ash	
	Beginning of flowering	End of flowering	Beginning of flowering	End of flowering	Beginning of flowering	End of flowering	Beginning of flowering	End of flowering
Root leaves . .	18·32	13·16	15·38	12·54	30·52	31·59	12·48	11·91
Lowest stem leaf .	8·22	6·14	6·64	5·26	32·29	34·81	12·15	11·66
Second ,, ,, .	9·78	7·32	7·94	6·76	35·30	36·77	11·65	11·61
Third ,, ,, .	11·52	8·80	9·60	8·70	35·79	36·68	11·36	11·33
Uppermost stem leaf .	14·54	13·26	11·58	10·52	36·65	37·65	11·20	10·74
Inflorescences . .	16·68	19·96	13·62	16·32	37·64	31·68	7·63	9·23
Stem proper . .	5·78	4·20	3·94	3·34	45·13	45·37	5·55	6·30

Figures from Christoph, Karl: Untersuchungen an *Dactylis glomerata* L., *Lolium perenne* L. und *Avena elatior* L. *Zeitschrift für Pflanzenzuchtung*, Bd. X., 1924–25, p. 311 (see Stapledon, 1927).

	Crude Protein		True Protein		Fibre		Ash	
Pasture .	Tall oat-grass	15·5	Golden oat-grass.	11·0	Cocksfoot .	28·8	Golden oat-grass.	10·7
	Timothy .	11·8	Timothy .	8·8	Timothy and Perennial rye-grass.	24·9	Crested Dogs-tail.	8·1
Range.		3·7		2·2		3·9		2·6
Hay .	Meadow Foxtail.	11·8	Meadow Foxtail.	9·7	Cocksfoot .	35·4	Meadow Foxtail.	6·8
	Tall Fescue .	5·5	Tall Fescue .	4·5	Meadow Foxtail.	28·7	Timothy .	4·1
Range.		6·3		5·2		6·7		2·7
Aftermath .	Crested Dogstail.	12·7	Cocksfoot	10·1	Cocksfoot	31·1	Golden oat-grass.	10·8
	Tall Fescue .	9·8	Tall Fescue .	6·7	Perennial rye-grass.	25·9	Meadow Foxtail.	8·5
Range.		2·9		3·4		5·2		2·3

True protein	Pasture Hay	9·9 5·1	4·8	Perennial rye-grass, and Meadow Fescue.
Fibre	Pasture Hay	26·4 34·5	8·1	Meadow Fescue.
Ash	Pasture Hay	10·7 4·7	6·0	Golden oat-grass.

During the past ten years a comprehensive study of forage plants, more particularly in relation to such morphological and physiological characteristics as affect their economic value, has been made at the Welsh Plant Breeding Station, Aberystwyth. These studies have been extended gradually to attributes such as self-fertility and self-sterility that have a direct and fundamental bearing on the production and propagation of improved strains.

To a very large extent workers in this division of crop plants are pursuing investigations in an entirely new field, and many of the results obtained up to the present necessarily represent attempts to establish basic facts whereon to build principles, without which breeding cannot proceed on scientific lines.

It is impossible to include anything more than a very brief summary of these extensive investigations here, and for purposes of illustration those on Perennial rye-grass and Cocksfoot only will be attempted.

Perennial Rye-Grass. The initial investigations with this grass consisted of experiments designed to ascertain the relative economic values of different nationalities of seed (Jenkin, 1930). In the case of rye-grass of British origin, two distinct lots were brought under observation—one ordinary Commercial seed, and the other Indigenous seed obtained from plants originally procured from old-established pastures.

Of two lots of Danish Pedigree Perennial rye-grass included in these observations one, Ba 34, approximated closely to the commercial group, but the other, Ba 52, was exceedingly lax in spring growth, while the flowering stems were of greater diameter, with few leaves and a generally wiry appearance.

A further sort included in these comparisons was Svalöf Victoria, which made very slow growth in early spring, but with warmer weather its development was vigorous, and throughout

the season it remained a darker green than other sorts. It was decidedly later than other forms in flowering, and the number of inflorescences was relatively low.

Very striking differences were observed between the English Indigenous and English Commercial, and the Irish and Ayrshire and Pedigree Ayrshire, which resemble the English Commercial. These were briefly as follows: the Indigenous gave an extremely dense turf of relatively short, glossy leaves in the early part of the year, and on the whole were not appreciably later in flowering than the ordinary Commercial. It exhibited a relatively low proportion of flowering stem to leaf, which was more pronounced as the plants approached maturity; the Commercial English, etc., were more lax in growth, and the leaves were longer than in the Indigenous, while at flowering time the proportion of stem to leaf was much greater. Towards maturity there was a greater tendency to withering in the basal leaves. In the aftermath these lots ran into inflorescence more readily than the Indigenous. When Indigenous and non-Indigenous lots were compared under pasture and hay conditions over two harvest years, the former outyielded the latter by 13 per cent., whilst at the conclusion of the second harvest year the Indigenous exceeded the non-Indigenous in tiller population by 50 per cent. In addition the indigenous material displayed a marked superiority to the non-indigenous on a persistence basis.

But although the various indigenous and non-indigenous lots when compared as units displayed differences of a constant and fundamental character, they all, regardless of origin, exhibited a high degree of variability, and by means of single plant cultivation it has been possible to study the individual components of both types.

The general position outlined with regard to Perennial rye-grass (and it applies equally to other grasses) is parallel to that existing in the case of cereals, where, in some populations of a particular "variety," forms may be selected with high tillering and low tillering capacities, with a tendency to the development of few or many fertile tillers and with many other small but distinct botanical and physiological attributes.

A test of hay and pasture yields was made in 1927–1929 with a number of commercial and indigenous forms. In this case an Aberystwyth Station pasture line, and Hawkes Bay, a New Zealand sort, were included. Presenting the figures of yield on the basis of British Commercial = 100, it was found that the British Indigenous again outyielded the Commercial both as hay and pasture; the Hawkes Bay was relatively high in hay yield, but was markedly inferior to Indigenous in pasture yield; the Svalöf Victoria did not reach the level of the British Commercial, the only feature of merit in this case being consistency of yield.

From individual plant studies the differences which can be regarded as established between the various Commercial and Indigenous lots irrespective of their origin show up in greater relief. These have been studied by Jenkin under the following heads: (*a*) behaviour in the seedling year; (*b*) date of emergence of inflorescence in the first harvest year; (*c*) production of flowering stems in the aftermath; (*d*) yield results with single plants; (*e*) stemminess of cut herbage (single plants).

Under (*a*) it was established that "commercial" seedlings make more rapid early growth than the "indigenous," but whilst tiller production was more rapid in the former up to two months from sowing, superiority in this respect later passed to the "indigenous," which ultimately formed the denser plants. The two major types also differed in the proportion of plants which produce inflorescences in the first year. Thus, treating various "indigenous" and "commercial" sorts as separate groups, while only 7 per cent. of the former produced inflorescences in the seedling year the corresponding figure for commercial was 24. At the same time the figure for two New Zealand sorts was 72 per cent.

(*b*) In the date of inflorescence emergence distinct differences are again evident, for while indigenous sorts varied from the 23rd to the 29th May, British Commercial varied from the 4th to the 9th May, and New Zealand sorts from the 6th to the 15th May. The corresponding dates for Station-bred (Aberystwyth) pasture types were 1st June and 3rd June.

It is noteworthy that the types with high tillering capacity are, as a rule, relatively late in inflorescence emergence. Con-

sequently, apart from the general indication of the type afforded by this feature, it may be utilized also as an indicator of the extent to which such a type is free from mixtures of earlier flowering types arising mechanically or resulting from cross-pollination.

(*c*) Observations under this heading show that the types that were relatively late in producing the first inflorescences tend to produce this set only, whilst the earlier types may produce an abundant quantity in the aftermath.

(*d*) The data found under this heading are amongst the most important economically, but, at the same time, owing to the biological differences of the various types it is desired to compare, difficult to obtain.

The following may be quoted as an illustration : if it is desired to compare, say, British Commercial and British Indigenous on a hay basis, the question of the exact date of cutting arises at once, for the difference between the dates of inflorescence emergence in these two types is at least fourteen days ; thus, to secure what are as nearly as possible comparable conditions, the dates of cutting must be somewhat arbitrarily fixed at the same number of days' lapse after inflorescence emergence. When this is done, however, the number of days allocated to aftermath growth must of necessity be shorter in the case of the slower-growing Indigenous. It is true that such limitations are incidental to the various sorts it is desired to compare, but equally true that where comparisons are made the results must be considered in the light of biological features peculiar to the material under review.

The following figures obtained by Jenkin, *loc. cit.*, may be quoted

Origin.	Number of Plants	Mean Emergence Date	Preliminary Cut	Hay Cut	First Aftermath	Second Aftermath	Total
Station-bred "hay"	50	6/5	167	123	140	156	144
British Indigenous.	50	21/5	99	137	136	83	118
British Commercial	75	7/5	100	100	100	100	100
Jaedersk . .	25	5/6	40	105	97	34	71

British Commercial = 100.

in some detail as they give additional data on the nature of the fundamental differences existing between Commercial, Indigenous and certain other sorts.

The Station-bred "hay" is notable for a high winter and early spring growth, and for excellent aftermath yields, which together place it well ahead of all the others in total yield. The Indigenous is remarkable for a lower early cut, but both the hay and the first aftermath yields are high, and the total yield is markedly superior to the Commercial. The Jaedersk being exceptionally late, gives a small preliminary cut yield, the hay figure is only slightly superior to Commercial, and the aftermaths are relatively small.

Under conditions resembling those of ordinary pasturing the following figures were obtained :—

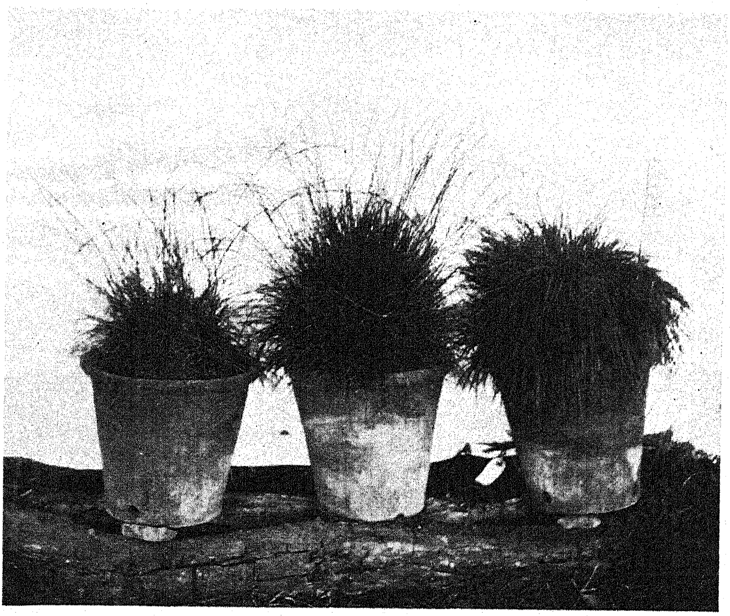
DATE OF CUTTING AND RELEVANT WEIGHTS OF CUTS

Origin.	8/4	8/5	3/6	2/7	29/7	26/8	22/9	All Cuts
Station-bred . .	149	189	221	214	228	182	180	178
Indigenous . .	116	118	150	144	155	145	156	131
Commercial . .	100	100	100	100	100	100	100	100
Jaedersk. . .	37	66	90	89	94	103	115	64

The Station-bred again secures a distinctly superior position throughout the whole period of experiment, whilst the superiority of the Indigenous to the Commercial is more marked under pasture conditions than it was under hay conditions.

A series of investigations similar in character and object to those just described has been carried out in New Zealand. There, as in Britain, Perennial rye-grass has been found to be composed of a number of types ranging in character from the dense, fine-leaved, multi-tillered form at the one extreme, to a form described as "False" Perennial. The latter is characterized by open crown and few tillers, and by stems with sparse foliation, whilst it approaches the true perennial in yield in the early months only, and recovers from cutting or grazing extremely badly.

PLATE VI



Illustrating three types of Perennial Rye-grass from one lot of seed of New Zealand origin; single plants taken from the field in the aftermath stage in the second year. *Left:* very stemmy type; *Middle:* type combining good leafage and considerable stem development; *Right:* type with no inflorescence in the aftermath.

(*By courtesy of T. J. Jenkin, Esq., M.Sc., Welsh Plant Breeding Station.*)

[*To face p.* 138.

One lot of New Zealand rye-grass (denominated Sandon) was grown at Aberystwyth in comparison with various British forms, with the following results :—

	"Pasture"	"Hay"	Total
Station-bred (pasture type) . .	197	—	—
Station-bred (pasture type) . .	192	166	177
British Indigenous	121	131	127
New Zealand (Sandon) . . .	138	114	124
British Commercial. . . .	100	100	100

It is particularly noteworthy that while the New Zealand lot is superior to Indigenous under " pasture " conditions, the latter is superior under " hay " conditions. Again, in the date of emergence of inflorescence the New Zealand is very similar to Commercial, and therefore distinctly earlier than Indigenous, indicating that the good pasture yield is not necessarily associated with a relatively prolonged period of growth.

A feature that may be found ultimately to be important in breeding work with Perennial-rye and other grasses is resistance to Leaf and Stem Rust, *Puccinia coronata* and *Puccinia graminis.* Bruce Levy and Davies (1930) observed a severe attack of the former and a slight attack of the latter in the early summer of 1930, during which the relative degree of resistance to attack proved an important feature. Thus, the Hawkes Bay rye-grass, the true perennial type, in comparison with the Southern seed, which is composed largely of the less perennial types, exhibited marked resistance. It was also observed that in the single plant cultures the dense leafy types are much more resistant to disease than the open, more stalky types. Italian rye-grass proper was fairly resistant to leaf-rust, but this was not the case with the less vigorous intermediate forms.

It is unnecessary to further emphasize the importance of these findings from the breeding aspect other than to express the view that the association of resistance with the most valuable forms of rye-grass renders the utilization of this character a relatively simple procedure.

Our knowledge of the feeding value of pasture grass has been extended in recent years by researches carried out under the ægis of the School of Agriculture, Cambridge University. Many subsidiary problems arising from the original investigations are still under survey, but the outstanding findings have been summarized by Woodman (1930, 1932), under whose direction the study has developed. It has been established that pasture grass in its young leafy condition has the character of a protein concentrate of high digestibility and nutritive value. Moreover, when pastures are adequately grazed, and the rainfall is sufficient to maintain growth, this character is maintained throughout the whole season.

A further most important finding is that under intensive grazing the high feeding value and the protein content of the grass are independent of the botanical character of the herbage, and of the presence of White clover (*Trifolium repens*).

In view of what has just been submitted with regard to the habit of growth, time of maximum vegetative development, and of the relative yields of hay and pasture of Commercial and Indigenous perennial rye-grass, the possible bearing of Woodman's researches on the breeding problem is apparent. The basal leaves of grass, *i.e.* the youngest shoots, are the most valuable because they contain a large quantity of protein in a readily digestible form, and under adequate grazing the development of a continuous succession of tillers in the grasses, and of stems and leaves in clovers is encouraged. This is a general effect irrespective of the species of the grass, but it may naturally be supposed to be more effective in those species and varieties which normally produce a greater abundance of tillers under any circumstances. Thus, in the case of Indigenous perennial rye-grass, whilst the tendency to produce flowering stems is clearly at a minimum, it exists concomitantly with a normal tendency to produce barren shoots in abundance, and these possess a high feeding value.

Having arrived at the most desirable types of Perennial rye-grass for the particular purpose in view, the breeder is then faced with the question of propagation. In the grasses this aspect of breeding procedure has revealed special features which, by reason of the lack of earlier work on the subject, have rendered the problem

peculiarly difficult. Grasses, for instance, are mainly chasmogamic, which fact involves the breeder in difficulties of propagation even in the relatively limited study of the progeny of selected plants. Jenkin (1931), who has studied the self-fertility of Perennial rye-grass in detail, has shown, however, that although this grass is mainly chasmogamic, the degree of relative self-fertility varies greatly in individual selections. Thus, in four plants he found that self-fertility varied from 0·8 seeds per 100 spikelets in one plant, to 117·6 seeds per 100 spikelets in another. He also found that the progeny of a highly self-fertile plant exhibits a high degree of self-fertility, and the possibility of obtaining a line with full self-fertility thus comes within the range of experimental possibility.

A further important aspect of his work is the discovery of plants exhibiting male-sterility, a phenomenon which appears to be co-existent with full female-fertility, for the male-sterile plants set seed abundantly when pollinated either artificially or openly. Male-sterility is exhibited in varying degrees : in one extreme of variation the anthers fail entirely to dehisce, in others there is a slight dehiscence at the distal end followed by the liberation of no more than a trace of pollen, while at the other extreme the anthers dehisce more freely and pollen is liberated, but the quantity is small compared with that produced by normal male-fertile plants.

The feature of male-sterility may have an important bearing in practical plant breeding, for Jenkin has been able to demonstrate that there is a strong tendency towards male-sterility in the progeny of plants exhibiting this feature. This, it will be observed, is paralleled by the high degree of self-fertility found in plants which are highly self-fertile. Moreover, male-sterile plants of Perennial rye-grass are particularly vigorous and for this reason there is a strong tendency to select them as basic parent plants. There is consequently a danger of the perpetuation of male-sterility, with the attendant liability to open pollination by differing forms, unless selection is directed to forms with a high degree of self-fertility.

A most important feature in the raising of improved strains of grasses is the loss of vigour attendant upon self-fertilization. Jenkin, *loc. cit.*, finds that self-fertilized plants show a reduction in

yield of 40 per cent. compared with plants produced by inter-crossing. This difference, Jenkin contends, may be due partly to less rapid, or even lower, germination in the case of selfed seeds, but what appears to be low total germinating power may be attributed to either slow or weak germination. In support of this contention Jenkin gives the result of germinating 27,201 selfed seeds from a very large number of mother plants as 83·9 per cent., whilst the germination of 28,988 seeds obtained from crossed plants was 92·9 per cent. The difference is indeed small when compared with that found in the yield. Unrelated plants, however, were ascertained to give the highest germinating capacity when inter-crossed, but except where the inter-crossed plants are closely related the germination is not greatly affected.

There seems to be little doubt from the figures supplied by Jenkin that the highest yield of produce is obtained from unrelated plants, and the lowest yield from selfed plants. Intermediate to these two conditions, but strongly tending to the higher yield standard, are plants resulting from crossing F_1 plants with selfed plants, and back-crosses, *i.e.* F_1 plants, with one or other parent. Nearly related selfed lines when crossed together are only very slightly superior to selfed plants themselves.

Cocksfoot. The problem of the improvement of Cocksfoot has been studied in great detail by Stapledon (1928, 1931) at Aberystwyth. In this case the study was developed in the form of an ecotypical survey of the species as influenced by the biotic factor—here the grazing animal as controlled by man, which Stapledon regards " as perhaps the master factor in influencing the vegetation of a preponderant proportion of the earth's surface."

The material studied by Stapledon was provided by collections of plants that were dug up from characteristic habitats, and by seed samples obtained from ordinary commercial sources ; of the former, 315 individual plants were obtained from representative habitats in England, Scotland and Wales and of the latter, samples were procured from Denmark, France, the United States of America, New Zealand and Britain. All this material was grown under carefully regularized and comparable conditions, the seed in sterilized soil, and the plants at wide but regular spacing, the

whole object of the comparisons being an attempt to arrive at the most valuable strains of Cocksfoot for agricultural purposes. In so doing the evidences of difference partake of the nature of "growth-form." Proceeding on this basis Stapledon classified his material according to the following major contrasting characteristics :—

(1) Density—Laxity. Here it was found that a dense plant produces a large number of tillers, and that both barren and fertile tillers grow away almost contemporaneously in the spring. At heading time, therefore, a dense plant shows a high proportion of comparatively large and well-grown barren tillers. Again, a dense plant flowers later than a lax plant and over a longer period.

In a lax plant on the other hand the barren tillers do not develop until the fertile tillers have made considerable development and in extreme cases not until the panicles are exserted. The fertile tillers are usually strong and vigorous, and flower more or less contemporaneously.

(2) Erect—Inclined. These terms refer to the position of the tillers at heading time—in some cases they are practically vertical and in others they grow away at a wide angle to the plant.

(3) Tall—Short. The height of the plant varies within wide limits.

(4) Rapidity of growth.

(5) Relative internode elongation.

(6) Ratio of leaf to stem.

(7) Bulk or yield.

(8) Earliness or Lateness. The range of flowering dates is a wide one. Although the dates of flowering of the various plants showed a yearly difference, the relation of individual plants to one another in regard to this feature remained remarkably constant from year to year.

In classifying the many forms brought under observation Stapledon employed six categories, viz., lax hay, dense hay, cups, tussocks, spreading pasture and dense pasture:

(1) Lax hay. Plants included in this group are tall with long

leaves ; the production of barren tillers is small, the plants make rapid growth and are early.

(2) Dense hay. Plants in this group also tend to be tall ; they are multi-tillered and produce a high proportion of barren tillers. They are late in flowering, but nevertheless make more rapid spring growth than any other of the dense forms, though they fall behind the lax hay sorts in this resepect.

(3) Tussocks are dense plants and intermediate in height between the hay and pasture groups. They tiller excessively and are characterized by considerable development of barren tillers. On the average Tussocks are late in flowering—slightly later than dense hay and nearly as late as the pasture groups.

(4) Cups. Plants in this group exhibit a wide inclination from the vertical of the early produced tillers, and there is not generally a very abundant production of contemporaneous barren tillers. There are two distinct sub-divisions of " cup " plants, viz., lax and dense types. The former, which flower early, approximate closely to lax hay, they tend to develop barren tillers only late in the season, and produce hay with a low percentage of leaf and of sheath. The dense cups are high yielding, and the production of barren tillers may be considerable. In the remaining two groups which embrace the pasture types, the plants are not tall and have relatively short leaves.

(5) Spreading pasture group. These are less dense than the dense pasture types, since many of the barren tillers develop after the elongation of the panicle shoots. As a general rule, the plants of this group are broader-leaved and broader-tillered than the dense pasture type.

(6) Dense pasture type. The plants of this group are sharply convex in outline and have a high proportion of barren tillers. The contribution of leaf, *i.e.* blade and sheath, to the hay is higher in this than in any other group, and the plants are particularly slow in growth in the spring.

Regarding the pre-eminent economic attribute yield, Stapledon was able to make several generalizations. He found, for instance, a distinct positive correlation between height and yield : thus on 1,147 plants representative of all groups the coefficient of correla-

tion was ·543 ± ·04. Dense pasture plants, although characterized by the greatest number of tillers, are not tall plants, and are not amongst the highest yielders, but the tussock types, although producing fewer tillers than the dense pasture plants, are taller and are the highest yielding. The dense hay plants, though not so tall as the lax hay forms, are decidedly heavy yielding, and with the tussocks constitute the most prolific plants.

The correlation between height and yield of plants constituting a single group is high. Thus, in a single group of dense hay plants it was ·693 ± ·032. "Within any one group the dense plants are invariably higher yielding than the more lax plants, while the same is true of whole groups in the case of closely related groups. Thus, dense hay outyields lax hay, tussocks outyield cups, and dense pasture usually slightly outyields spreading pasture."

The bearing of the type of a Cocksfoot on its value for hay production is set out by Stapledon in the form of yield trials conducted during four years 1922–1925. In these Danish, French, New Zealand and Indigenous were compared under broadcast and drilled conditions. The total yields for the four years were as follows :—

	Broadcast	Drills
Danish	179·8	150·1
French	135·8	95·5
New Zealand	188·9	168·5
Indigenous	155·0	163·9

Two important features are emphasized in these tests: the first that the New Zealand and Indigenous are relatively more productive in the condition of drilled seeding, and the second that whereas the yield of the Danish and French becomes rapidly smaller from the second to the fourth season, that of the other two sorts decreases at a much slower rate.

When the proportion of shoots bearing inflorescences and leaf shoots only is determined, differences of a still more fundamental character are established as follows :—

		Panicle Shoots	Leaf Shoots
Danish . .	1924	59·6	40·4
	1925	50·3	49·7
French . .	1924	47·9	52·1
	1925	56·0	44·0
New Zealand .	1924	36·6	63·4
	1925	26·0	74·0
Indigenous .	1924	39·3	60·7
	1925	37·1	62·9

In summing up the relative value of the two groups—Danish and French on the one hand and New Zealand and Indigenous on the other—Stapledon is led to conclude, however, that the lighter hay crops produced by the strains exhibiting the higher leaf-shoot stem-shoot ratio is more pronounced under conditions of lessened soil fertility. Inversely, such strains make a relatively greater response under conditions of greater soil fertility and of higher manuring.

Having defined the form and character that the various types of Cocksfoot may assume, the procedure adopted in raising seed must depend upon the extent to which self-fertility is or is not the normal rule, and whether under the condition of self-fertilization other considerations such as loss of vigour operate to the detriment of the final economic result.

As the outcome of selfing more than 1,200 plants of Cocksfoot in comparison with plants subjected to open pollination, Stapledon concludes that on the average cross-pollination is six to ten times as effective as self-pollination when the viable seeds produced per panicle is the standard of comparison. But the capacity for self-fertility in individual plants varies within so wide a range as from complete self-sterility to approximately complete fertility. In some cases, plants which have been selfed for five generations have produced individual families every plant of which has been highly self-fertile.

Cocksfoot considered as a species may be regarded as possessing a higher degree of self-fertility than many other herbage crosses,

and there is good reason to suppose that completely self-fertile lines can be isolated. The fact of this high degree of self-fertility makes it highly probable that different plants encaged for cross-pollination purposes may undergo a certain amount of selfing.

In view of its important practical bearing, the observations on one plant may be given here. A mother plant, No. 694, derived from Commercial seed obtained from Denmark, when selfed up to L 4, gave families of outstanding purity in respect of colour of the foliage, growth form and panicle characters; the majority of the families have maintained vegetative vigour.

Plant No. 694 when selfed proved also to be a very heavy, probably the heaviest, seeder. The best looking and the poorest looking of the L 1 plants were selfed, when the former gave an exceptionally high yield of seed, and the latter a relatively poor yield. This segregation was maintained in subsequent generations, for only poor seed yielding plants were obtained from the original poor L 1 plant. The high yielding plant gave rise to progeny all of which were either high or very high seed yielders. The best looking plant from the highest seed-bearing plant in L 3 was selfed and again gave a family considerably above the average. The total number of selfings was small, but so far as they go they furnish evidence of definite segregation into high and low seed-producing families.

As indicated earlier, the value of selfed plants will be determined largely by the loss of vigour that may result from this procedure. On this aspect, Stapledon's investigations indicate that, on the average, cross-fertilized plants of Cocksfoot are twice as vigorous as when self-fertilized. This conclusion, however, is applicable only to particular individuals, and segregates may occur in L 1 which are equal to normal F_1 plants in vigour.

When robust plants are selfed in all generations there appears to be little loss in vigour after F_1. On the other hand, propagation of poor families by selfing leads to progeny which exhibits a cumulative loss of vigour, ending finally in total extinction. Some of the growth forms of Cocksfoot remain true to type under selfing.

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CHAPTER VII

RED CLOVER (*TRIFOLIUM PRATENSE* L.) and WHITE CLOVER (*TRIFOLIUM REPENS* L.)

Red Clover

THE Red clovers in use to-day are grouped in three divisions, early flowering, late flowering, and wild red. The outstanding differences existing between the early and late flowering sorts have been a matter of common knowledge to agriculturists for a considerable time. The seed of the two sorts, however, originated in the past partly in the British Isles and partly in other countries, and early investigations were confined mainly to determining the relative values of the " nationalities " of this plant.

The early Red clovers used in the British Isles are English Broad Red, Vale of Clwyd (early form), Canadian, New Zealand, American medium, Chilian, Brittany, French, Italian, Czecho-Slovakian, Silesian and Polish, whilst the sources of the late flowering clover seed, apart from the four endemic British varieties, Montgomery, Cornish Marl, English late and Vale of Clwyd (late form), are America (American Mammoth), Canada (Altaswede), Sweden, Denmark, Norway, Poland and Russia.

The outstanding feature of difference between the early flowering and the late flowering is indicated by these two denominations, but the early flowering sorts are characterized in addition by laxness and erectness in growth, whilst the late flowering are denser and more prone to be prostrate in growth. Agriculturally, however, a very important difference between the two sorts is their relative persistency, for while the early flowering sorts are in the main biennials, the late flowering may be regarded as short-lived perennials, since they frequently last into the third or fourth year. Thus, in practice the early flowering sorts are essentially adapted to short leys, and the late flowering to longer leys.

To these characteristic differences in rate of growth may be attributed the fact that whilst the early flowering sorts commence growth early in the spring and flower early, they also produce a good aftermath; the late flowering sorts, on the other hand, remain winter dormant longer, and produce little or no aftermath.

The following relative yields of hay and aftermath from various clovers grown at Aberystwyth in 1921–1927 illustrate the differences just mentioned:—

	1921	1923	1924	1925	1926	1927
Late Clovers—						
Montgomery	100	100	100	100	100	100
English	104	107	63	110	120	—
Swedish	96	88	123	—	65	104
American Mammoth	64	85	84	—	104	76
Early Clovers—						
English Broad Red	111	62	47	70	58	58
American Medium	79	65	69	—	—	66
Chilian	86	48	—	—	—	—
Italian	39	20	—	—	—	—
Wild—						
Indigenous	—	84	58	—	75	—

The comparisons of various home-grown and imported clovers have indicated that as a rule native clovers are more productive and persist longer than imported varieties, and a survey of similar comparisons in other countries indicates that this is a conclusion common to them also.

The value of this critical work extends far beyond this generalization, for it has been instrumental in establishing the existence of valuable-indigenous sorts, which differ to some extent morphologically but, more important still, in physiological attributes such as persistence and adaptation to defined soil conditions. They also differ in the extent to which they can withstand grazing. Thus, although many of the different sorts of both early and late flowering clover each in their respective class exhibit a conformity to the general type of that class, they also exhibit differences which furnish a valuable basis for selection. As a result of such selection

it may be possible not only to enhance the value of a particular kind for the district in which it is now localized, but to extend its use to other districts.

The improvement of Red clover either by selection of individual plants or by hybridization necessitates as a fundamental datum a full knowledge of the extent to which it is self-fertile, and on this point the investigations of Williams (1925, 1931) at Aberystwyth have provided results of a most informative character. Williams' conclusions are that for all practical purposes Red clover may be regarded as self-sterile; autogamously Red clover produces very few seeds. Thus from 158 plants protected from insects and producing 3,163 flower heads during the years 1921, 1922, 1924, 1925 and 1927, only 57 seeds were obtained, or an average of 0·018 seeds per head. When artificially selfed during seven seasons, 35,175 florets from 262 plants yielded 300 seeds, or ·85 per cent. per flower pollinated. Of the 262 plants 237 did not produce a single seed, the 300 seeds obtained being contributed by 25 plants ; of these, 19 plants produced 1 to 7 per cent. of seeds, 5 produced 9 to 30 per cent., and the remaining plant gave on one occasion 74·7 per cent. of seed. Thus, it may be concluded that the majority of Red clover plants are self-sterile.

The 1 self-fertile plant that Williams found was an F_1, No. 344(1) 263, and this in comparison with 5 other plants of the same family was tested for self- and cross-fertility in 1928, 1929 and 1930, with the following results :—

	1928		1929		1930	
	Crossed	Selfed	Crossed	Selfed	Crossed	Selfed
Plant No. 261	62·0	0	30·7	0	—	—
,, 262	—	0	59·1	0	—	—
,, 263	49·1	74·7	62·9	30·0	32·1	42·1
,, 264	16·3	0	39·3	0	—	—
,, 265	67·5	0	19·8	0	—	—
,, 266	62·4	0	47·4	0	40·4	0

Passing to the question of the crossability of unrelated plants :

it was found that out of a total of 416 pollinations made between unrelated plants 401 were fertile; out of a total of 108 reciprocal crosses, 103 were fertile, in 4 cases one parent was fertile in one direction, and in 1 case the crosses in both directions were infertile. Out of 308 crosses made in one way, 298 were fertile and 10 were infertile. Williams, however, considers that in the 10 cases of apparent infertility the non-setting of seed may be due to an unhealthy condition of the plant rather than to true incompatibility.

In the case of sister plants there was evidence of definite reciprocal cross-compatibility, and of reciprocal cross-incompatibility: of 475 $F_1 \times F_1$ sister crosses, 333 were cross-compatible and 142, or 29·9 per cent., cross-incompatible; of 113 $F_2 \times F_2$ sister matings 71 were cross-compatible, and 42, or 37·1 per cent., were cross-incompatible.

The technical difficulties attending the artificial cross-fertilization of clover are many and very obvious, and within recent years breeders have resorted to methods which enable them to utilize the services of the humble bee in their investigations. From observations it has been found that the pollination of Red clover is effected almost entirely by six species of this bee—*Bombus agrorum* and *Bombus horterum* being the most numerous and in consequence the most important. The cause of failure of the seed to set is believed to be due to the robber bees, *B. terrestris*, *B. lucorum* and *B. sorsensis*, which secure the honey of which they are in search by puncturing the flower somewhat near its base, whereby the flower loses the advantage of pollination usually secured when the bee obtains the honey in the more usual manner by inserting its proboscis through the mouth of the flower.

By ridding bees of all pollen adhering to their bodies, and then introducing them into insect-proof chambers in company with the plants it is desired to cross, the previous difficulty of securing fertilization has been reduced greatly.

Thus, in 1929 and 1930 the results on the top of the next page were obtained; if the number of florets per flower head is taken at 105, the high rate of seed production secured by this method is obvious.

	No. of Crosses	No. of Plants	Average No. of Seeds per Plant
1929	17	275	509
1930	8	77	323

Many of the problems attending seed production having been elucidated, we arrive at once at the question of producing improved varieties. This, according to Williams (1931), is being attempted in three ways: by (1) strain building, (2) brother × sister crossing, and (3) diallel crossing. The procedure in regard to (1) consists of crossing plants of a small number of families that are similar in their agricultural features, and this method meets the immediate demand for improved material. The method adopted under (2) involves the expenditure of longer time and more intensive selection.

The F_1 progeny of selected pairs of plants are usually very uniform in appearance, but nevertheless on closer analysis they exhibit a high degree of variability. These differences become more apparent when the F_1 plants are inter-crossed, and although the F_2 progenies retain the distinctive appearance of the F_1s they invariably exhibit a wide range of segregation. If plants from the best families are selected and inbred, and the process of selection and inbreeding repeated for a number of generations, a high degree of uniformity is reached ultimately.

This method of breeding is attended with considerable loss of vigour, which, however, may be regained by re-crossing with the best plants of the best but unrelated families. It may be noted that inbreeding between cross-compatibles has no direct effect on fertility or on the size and quality of the resulting seeds, and the undesirable effects in this case appear to be confined to loss in the vigour of the plant.

Some combinations of plants will always produce better progenies than others, and the object of diallel crossing (3) is to determine which plants and families when crossed show the best performance. This is done by observing their progenies in the field, and when this is ascertained combinations involving the

best families raised under controlled conditions of fertilization are attempted.

It has been shown by the investigations of Jost (1907), Martin (1913), and Silow (1931), that self-sterility in Red clover is due to the slower growth of " self " pollen than of foreign pollen in the stylar tissue, and that this may be accounted for by an inhibiting action of that tissue.

Williams, *loc. cit.*, concludes from the evidence of his various crossings that self-sterility and cross-sterility in Red clover may be due to a series of multiple allelomorphs and that his data support East and Mangelsdorf's hypothesis of oppositional factors. This hypothesis postulates that the growth of the pollen tubes is rapid in styles bearing different sterility factors, and slow if the factors in the pollen and styles are the same. A plant of the assumed genetic constitution S_1S_2 is not only self-sterile, but is also reciprocally cross-sterile with all other plants of the same constitution, but reciprocally cross-fertile with plants of the constitution S_1S_3 or S_3S_4.

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White Clover

Although White clover was well known to agriculturists about the beginning of the eighteenth century, it is only within the past thirty years that the botanical composition of the various forms of the plant in general cultivation or found growing in a wild condition have come under critical survey. The impetus to these investigations arose mainly from the results of certain experiments in the improvement of poor grass land, designed and carried out by the late Professor Sir William Somerville (1902). The early experiments were commenced by Somerville at Cockle Park Farm, Northumberland, in 1897, and included a series of plots to which basic slag, at that time a waste product produced in large quantities at the steel furnaces in north-eastern England, was applied. The improvements in the stock-carrying capacity arising from the use of basic slag on this class of land were extraordinarily rapid, and were related to the remarkable development of White clover which followed its application. In many cases the improvement occurred on permanent grass land on which no clover seed of any description had been sown, or known to have been sown for many years.

These findings directed attention to the persistency of certain types of White clover which, although known to some agriculturists long before this time, had not received general recognition.

Botanically, White clover may be divided into two main groups : (1) the ordinary White or Dutch clover, *T. repens* race *hollandicum*, and (2) Wild white clover, *T. repens* var. *Sylvestre*. The former was most probably introduced into England from Holland in the seventeenth century. It is a larger plant than the Wild white sort in every way, but does not grip the ground to the same extent and consequently does not form the dense growth usually associated with that form. While White or Dutch clover produces heavier yields than Wild white, it lacks the persistency of that sort (Armstrong, 1931; Ware, 1925),

The Wild white form, in addition to being smaller in leaf, stem and flower, displays a much more prostrate habit of growth, and a greater spreading range than the White Dutch. It consequently

finds its highest value as a pasture plant, while White clover can be used with greater advantage in temporary leys.

White clover commences growth in the spring earlier than the wild form, and produces a greater quantity of edible material; the Wild white is much more of a summer and early autumn plant.

When single plants of either of the two main sorts are compared it is found that they both present the characteristics of aggregations or populations, the individual units of which exhibit small but constant morphological and physiological differences. In some cases it has been found that types of Wild white clover derived from definite habitats are in reality ecotypes, and consequently the maximum benefits from their use are realized only when the new conditions in which it is desired to grow them approximate those of the original habitat. In New Zealand, for instance, six types have been recognized and described, namely, Type 1, New Zealand Wild White, No. 1; Type 2, New Zealand Wild White, No. 2; Type 3, ordinary New Zealand White; Type 4, Lax early-flowering New Zealand and ordinary European White; Type 5, Kentish Wild White; and Type 6, Ladino White. Each of these possesses a definite form, and other attributes such as persistency, ability to thrive in competition with other herbage plants and high or low productivity peculiar to the type (Davies, 1931).

Type 1 is characterized by large leaves, stout stolons, has a wide spread, and is highly productive; it is also fairly persistent. On the best pasture land in which the competition of plant with plant is extremely keen, this type of clover has exhibited a marked ability to maintain itself and furnish a large produce.

Type 2 has a smaller leaf than Type 1 and a somewhat lower production value, but is distinctly valuable on good average grassland soil.

Types 3 and 4 partake of the nature of annuals. They establish themselves readily and then make rapid growth, but after seeding, which is relatively quick, they die away more or less rapidly.

Type 5, the Kentish Wild White, has a high persistency value, but fails to compete successfully with the other herbage plants constituting the turf of the first-class grassland which is largely utilized as cattle pasturage. Nevertheless, on typical sheepland

which does not reach the fertility standard requisite for the production of the higher yielding types such as 1 and 2, Kentish Wild White fulfils a useful *rôle*.

The very well-marked differences existing in these few types are indicative of the lines followed in initial breeding investigations with this plant. It is possible and very highly probable that even in such types as those represented by Nos. 1, 2 and 5, individual unit forms may be isolated which are superior, at least in some features, to the parent population in which they are found. Such superiority may partake of the nature of greater adaptation to certain habitats, and if so will ultimately contribute to a wider range of economic utility.

Investigations of this and similar character form the initial basis of future improvement, and having once selected the best existing forms further improvement lies in objective breeding.

As in the case of Red clover, however, the extent to which improvement is possible will be determined very largely by the degree of cross-fertility of the various selected forms. Williams (1931) as the result of his investigations of this problem has come to the conclusion that White clover, although as a rule highly self-sterile, is not so self-sterile as Red clover. Out of 130 plants which were protected from bees in 1927 and 1928, he found that 15 produced seed, but only 102 seeds were obtained, or the equivalent of an average of 0·058 seed per flower head.

By artificially self-pollinating 104 plants in 1928 and 1929 the same investigator obtained 383 seeds from 27 plants, an equivalent of 3·3 seeds per 100 florets. Comparing these results with those obtained from similar pollinations of Red clover, on the basis of the number of seeds produced per 100 florets selfed, the following figures are relevant :—

1928	Self-fertility	of	White clover	= 2·1	per cent.
,,	,,	,,	Red clover	= 0·69	,,
1929	,,	,,	White clover	= 5·4	,,
,,	,,	,,	Red clover	= 1·14	,,

Of the 27 plants which produced seed in 1928 and 1929

	20	gave	only	1 to 10	per cent.	seed.
	6	,,	,,	15 to 26	,,	,,
and	1	,,	,,	102·5	,,	,,

As in the case of Red clover the appearance of highly self-fertile individual plants is noteworthy.

Proceeding to the cross-fertility of unrelated plants: Williams found that out of 155 such crosses made in 1927–1930 only 8 could be classified as cross-sterile, and of these 8 the failure to set seed in 6 cases was probably due to disease; consequently in 2 cases there is strong evidence of genuine cross-incompatibility.

In a series of reciprocal tests 33 crosses were made, and in 32 cases these proved to be reciprocally cross-fertile. In the case of the single failure to cross reciprocally a condition of diseased pollen may have been a contributory cause of the result. On the whole of the evidence, cross-incompatibility between unrelated plants may be regarded as a rare phenomenon.

In the case of sister plants, out of 137 crosses 101 were found to be compatible and 36 incompatible. In the compatible matings most of the plants were either reciprocally cross-compatible or reciprocally cross-incompatible.

A further series of crosses between unrelated plants and between compatible sister × sister crosses suggests that there is no significant difference in fertility between the two crosses.

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CHAPTER VIII

ROOTS—MANGELS, SWEDES AND TURNIPS

A NOTABLE feature in the development of Danish agriculture in recent years is the extension of the area devoted to the root crops, mangels, swedes and turnips. In 1861 this was 6,000 acres; in 1871, 16,600 acres; in 1881, 45,700 acres; in 1901, 330,000 acres and in 1919, 678,000 acres. In 1918 while the acreage devoted to these root crops in Great Britain was equivalent to 5·4 per cent. of the total acreage under crops and grass, in Denmark it was no less than 9·7 per cent.

To a very large extent this fundamental change from a farming system involving a large proportion of fallow land to one in which the normal fallow occurring in a rotation was replaced by a root crop may be attributed to the work of N. J. Fjord (1825–1891), a lecturer at the Royal Agricultural College of Copenhagen. As is the case with so many valuable inquiries undertaken in Denmark, the initiative was taken by the farmers themselves. The underlying cause that led them to seek an answer to the question as to how far they could utilize roots as a food, particularly for milch cows, is not generally stated, but some of the reasons can be readily imagined. For instance, from about the middle to the end of the last century it was a general custom for many of the largest Danish farmers to send their sons to farms in England and Scotland for a period of tuition. There they had an opportunity of studying systems of farming, other than their own, in operation, and they cannot fail to have been struck by the extensive cultivation of root crops which in 1881 occupied no less than 13 per cent. of the arable area of Great Britain, as compared with two-thirds of 1 per cent. in their own country.

The use of roots as fodder for milch cows soon became a matter of serious discussion in Denmark. Realizing the necessity for

reliable information on feeding value, a number of leading farmers induced Fjord to undertake experiments that would supply data capable of being used as a reliable guide in determining future policy with regard to these fodder crops.

Detailed accounts of Fjord's experiments appeared as his investigations progressed, and a summary has been published by Faber (1920). The basic result of Fjord's investigations was that 1 lb. of solids in roots was found to be equivalent in feeding value to 1 lb. of corn; thus, taking the average yield of barley at $4\frac{3}{4}$ quarters, and of swedes at 19 tons per acre (which were the average figures of yield for Denmark in 1909–1913), and assuming that there is 12 per cent. of solids in swedes, a crop of barley will produce 1,900 lbs. of foodstuff, but 19 tons of swedes will yield 5,100 lbs. of solids, or two and a half times as much.

Without digressing too far from the main subject, it may be pointed out that Fjord also showed that roots could be used for milch cows without impairing either the yield or quality of the milk in any way, while the weight of the cow was increased during the experimental period.

The effect of adding mangels to the food, taking the average of six farms during a three-year period, calculated per 100 lbs. of mangels, was :—

to increase the yield of milk by	6·3 lbs.	per cow per day.
to increase the weight per cow by	1·1 ,,	
to reduce the straw consumed by	7·0 ,,	

The effect of adding 125 lbs. of turnips per day was

to increase the yield of milk by	3·0 lbs.	per cow per day.
to increase the weight per cow by	0·7 ,,	
to reduce the straw consumed by	1·0 ,,	

The smaller effect produced by the turnips bears a close relation to the analyses of the two kinds of roots used in the particular tests from which the figures were obtained, thus :—

	Sugar per cent.	Total Solids per cent.
Mangels .	7·54	12·96
Turnips .	3·28	8·88

Almost at the same time as Fjord commenced his feeding experiments, the Society for Improving Cultivated Plants began to direct serious attention to the root crops with the intention of ascertaining which varieties, and which individual strains of a variety, were the most valuable on the basis of the yield of solids per acre. These investigations were placed under the direction of L. Helweg, who published the first account of his work in 1886, from which date until the present time reports have been made annually.

Helweg at a very early stage found that not only varieties but strains of individual varieties differed in the total solids found in the root, and in order to test the effect such differences might exert on feeding value he co-operated with Fjord in an actual feeding trial. This particular test was made with Eckendorf and Elvetham mangels fed to pigs on two farms, at one of which the crop of Eckendorf was fairly high in sugar and total solids, and at the other low in both constituents. The Elvetham was grown at one farm and produced high sugar, and high total solids contents. Thus :—

		Sugar per cent.	Total Solids per cent.
Eckendorf.	First farm .	8·8	12·7
	Second farm .	4·5	9·3
Elvetham	. . .	10·0	14·8

The average increases in weight per pig in ten days were as follows :—

First farm	(two groups)	.	8·6 and 8·9 lbs. respectively
Elvetham	(,, ,,)	.	8·7 and 8·6 ,, ,,
Second farm	(,, ,,)	.	7·6 and 8·4 ,, ,,
Elvetham	(,, ,,)	.	8·9 and 9·3 ,, ,,

These results, and others furnished by Fjord from time to time, were sufficient confirmation of the basis on which Helweg commenced his efforts to raise the value of the Danish root crops.

To understand and appreciate Helweg's procedure it must be

pointed out that the raising of root crop seed in Denmark and other countries is almost entirely in the hands of private seed firms, to whom the agricultural community are indebted for most of the improvements that have been effected with these crops. In practice, mangels, swedes and turnips may each be regarded as populations of vast numbers of cross-fertile forms, differing to some extent morphologically and physiologically, and in such important economic attributes as yield of roots per unit area, and in the composition of the roots. It has been shown repeatedly to be possible to isolate from these populations individual roots which when selfed will retain in a high degree of purity various attributes whether physiological, morphological, quantitative or qualitative. But the retention of any particular attribute in a condition of relative purity demands freedom from inter-crossing with inferior strains. Selfing, on the other hand, frequently entails a high degree of sterility, and of greatly reduced vigour of the progeny; consequently strain building entails the crossing of parent roots which have been ascertained by progeny tests to possess values of a genetic character—in other words, a high ascertained value that is not due to mere fluctuation. It has been found possible by careful selection on a dry matter basis to select parent roots which exhibit superiority in this respect, and by repeated selection of their progeny to produce new strains exhibiting a still further superiority. All these advances, however, must be made concurrently with other requirements such as resistance to disease, keeping quality, and, in the case of mangels, ease in lifting.

A general increase in the size, and consequently the yield, of roots is the most spectacular advance that has been made, but unfortunately such a change is frequently unrelated to the quality of the root, and the final result is that, although a superior yield is obtained, the true value of the crop per unit area for feeding does not show a corresponding improvement.

With a larger number of breeders working on the same crop, each with his own particular ideas as to the best conformation of a root crop, and only agreeing on the major test of yield of roots per unit area (which, however, was almost invariably regardless of

Variety	Average Yield of Dry Matter in cwts. per Acre.			Number of Strains tested. Annual Averages.		
	Class I.	Class II.	Class III.	Class I.	Class II.	Class III.
Mangels—						
Barres	60·0	57·2	53·3	6	10	5
Elvetham	59·1	56·5	53·5	4	7	4
Eckendorf	55·2	53·8	49·6	4	6	4
Swedes—						
Bangholm	60·9	—	52·5	1	1	3
Turnips—						
Yellow Tankard . . .	33·9	31·2	28·8	3	4	4
Funen Bortfeld . . .	33·3	31·0	27·5	2	3	3
Carrots—						
Champion	46·2	43·3	40·4	4	5	3
White Belgian . . .	47·8	—	41·4	3	5	2

true feeding value, namely, dry matter per unit area), it was only to be expected that the number of varieties and strains of varieties in use would necessarily be a very large one. Helweg's work was a critical evaluation of these many units on a dry-matter basis.

As already pointed out, the experiments have been in operation for a long series of years, and it is not possible here to indicate more than the general results. To commence with mangels: three classes of mangels were found in general cultivation in Denmark in the early years of the tests, namely, Barres, Elvetham and Eckendorf. Barres, an oval, yellow mangel, is stated by Vilmorin (1923) to have been selected from the German Yellow Mangel, a long form, by Louis de Vilmorin. From the same parent an intermediate form, de Vauriac, was raised by M. Gay. Another oval-shaped yellow mangel appears to have been produced in Scotland by Messrs. Peter Lawson & Son. In general appearance Vilmorin and Lawson's oval yellow were strikingly similar, and are known in Denmark under the denominations Vilmorin Barres and Lawson Barres, but as a general class Barres only. As a class Helweg defined the Barres as follows: a longish or oval-shaped, orange-coloured mangel; length generally a little more than double the width, the largest diameter being found a little above the middle. The flesh is white with a faint yellow tinge, and the stalks of the leaves are green, not yellow.

The Elvetham was a long, English variety which Vilmorin considers to have the same origin as a German variety, Disette d'Allemagne.

The Eckendorf was a tankard-shaped mangel produced in Germany by Von Arnim. In this class there are yellow, red and white forms.

Of these three classes no less than fifty strains were tested in the period of six years 1894–1899, and the average yields of dry matter per acre are shown in the following table.

Those strains which fell in the highest third were considered Class I; those in the lowest third Class III, whilst Class II comprised those strains which fell between the other two classes.

The average yields in cwts. of solids or dry matter per acre for Classes I and III were :—

	Mangels	Turnips	Carrots
Class I .	58·1	33·6	47·8
Class III .	52·1	28·2	40·9
Difference . .	6·0	5·4	7·9

which, taking barley at 30*s*. per quarter (or 4 cwts.) is equivalent to a difference in favour of Class I of

Mangels	Turnips	Carrots
37/6	33/9	49/4

In addition to the differences established between the three main varieties of mangels, the continued comparisons of Vilmorin Barres and Lawson Barres indicated the consistent superiority of the latter in dry matter per acre.

These findings led to several important changes; first, there was a very significant alteration in the relative areas devoted to the different sorts of mangels, which may be gauged by the quantities of seed sold. According to Helweg's estimate the following figures are a measure of the changes which occurred between 1884 and 1915 :—

	Seed sold	
	1884 per cent.	1915 per cent.
Of Barres . .	21	88·5
,, Eckendorf . .	6	9
,, Elvetham . .	61	2
,, Other varieties .	12	0·5

Secondly, there was the change over to the Lawson Barres, already mentioned, and, thirdly, the concentration of selection on progenies of Lawson Barres, leading eventually to the production of strains of this mangel which exhibited a superiority to the earlier

strains experimented with. Examples of these are Ferritslev, Rosted and Sludstrup, the first two being selections of Lawson Barres, and the latter a strain obtained by crossing Lawson Barres and Vilmorin Barres.

With regard to swedes and turnips, progress comparable to that made with mangels was achieved with these two crops; it was found, for instance, that Yellow Tankard was the best variety of turnips and Bangholm was equal to the best of the swedes.

A yellow-fleshed turnip, Bortfeld, was ascertained to be a particularly rapid growing form, and is now grown largely in Denmark as a competitor to Yellow Tankard.

In the tests of 1914–1915 fifteen strains of swedes were included of which six appeared in Class I, three being of the Olsgaard strain, two of Pajbjerg and one Lyngby. All these swedes are of the Bangholm type, but they exhibit qualitative and quantitative differences, for while the Olsgaard and Lyngby strains produce a high yield with lower percentage of dry matter, the Pajbjerg strain produces a large percentage of dry matter, and a somewhat smaller yield of roots.

The value of certain selections of some of these types has been enhanced by the selection of strains that are resistant to " Finger and Toe " disease (*Plasmodiophora brassicæ*). From the Pajbjerg, for instance, which is susceptible to that disease, Studsgaard Bangholm and Herning Bangholm, both resistant to it, have been obtained. Certain tests of these two strains carried out on infected land in North Wales in comparison with some British varieties demonstrated certain interesting features: it was shown, *inter alia*, that the yield of Herning Bangholm was inferior to Magnum Bonum, but in actual feeding value the position of the two varieties was reversed, for whole Magnum Bonum produced 1 ton 6 cwt. 3 qr. of dry matter per acre, Herning Bangholm yielded 1 ton 9 cwt. 1 qr.—a superiority of more than 2 cwts. of dry matter per acre.

The resistance to " Finger-and-Toe " in the two strains under test did not appear to be directly related to the quantity of dry matter or to the amount of sugar present. The resistant strains also suffered less from Mildew than the British sorts grown in

comparison with them, and finally showed a marked superiority to other varieties in keeping value.

Further trials were conducted in Mid-Wales in 1925–1927, and included another resistant strain, Wilhelmsburger Otofte. The superior resistance of the Danish forms was demonstrated again, with the result that they gave a definitely higher yield on disease-infected soil. Their superior resistance to Mildew was also again evident. At some experimental centres the difference between a resistant and non-resistant swede amounted to an economic return in the one case, and a complete failure in the other.

There was some evidence that the Wilhelmsburger Otofte was somewhat more resistant than the Studsgaard Bangholm and the Derning Bangholm strains (Whitehead, 1920–1921, 1925; Davies, Griffith and Evans, 1928).

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PART II

CROPS OF THE SUB-TROPICAL AND TROPICAL REGIONS

CHAPTER IX

BEVERAGES

COFFEE (*COFFEA spp.*)

THE coffee of commerce is derived from a number of species of the genus *Coffea* of the natural order *Rubiaceæ*. The genus consists, according to Chevalier (1929), of some fifty species indigenous to tropical Africa. Of these he recognizes as of economic importance some ten which are, for the most part, inter-fertile. Of these ten, five contribute the major portion of the commercial product. Cramer, in a series of articles (1918, 1919), has given an account of the forms grown in the Dutch East Indies.

The use of coffee appears to have been known from prehistoric times to certain of the indigenous races of Africa, and it is only in recent times, about the sixteenth century, that the cultivation extended to Arabia. In later times the so-called Arabian coffee has been carried to all tropical countries having suitable climatic conditions, notably to Ceylon, Java and Brazil. Owing to the susceptibility of the Arabian plant to disease, of which the complete destruction of the Ceylon industry by *Hemileia* is an outstanding example, other, more robust, species have been cultivated in recent years, but the major portion of the product is still derived from the Arabian plant.

The more important species are :—

C. arabica L. A small tree 8 to 25 feet, with small berries and growing at 3,000 to 6,000 feet. Probable home Abyssinia.

Numerous varieties are recognized, the mutational origin of some of which is on record.

C. liberica Bull. in Hiern. A large tree 40 to 50 feet, with big berries growing at low altitudes. Probable home West Africa.

C. excelsa Chev. A medium-sized tree with small berries. First discovered in 1904 by Chevalier near Lake Tchad. Its cultivation has been extending in Java and Tonkin owing to the quality of the product and the high yield.

C. canephora Pierre. Typical of the "robusta" group of coffees. Shrubs and small trees with branched stems and small seeds. Indigenous to a wide stretch of country centred on the Congo basin. It appears to have been cultivated from time immemorial by the indigenous races and exists in many forms. Owing to its resistance to disease, especially *Hemileia,* and its high yield, it has been widely introduced, but the quality of the product is poor and only used in blends.

C. stenophylla G. Don. A small tree 10 to 15 feet high, with small seeds. It is the highland coffee of Sierra Leone, to which country and French Guinea it is indigenous.

Mention should also be made of *C. congensis* Froehn., a native of the Congo basin which, though of small direct economic importance, has been used in Java and Porto Rico to raise hybrids.

The coffee plant is a perennial, bearing opposite leaves. The branching system is dimorphic and has been studied by Arndt (1929), whose account has, however, been criticized by van Hall (1930). The flowers are borne in clusters in the leaf-axils of the oblique branches and their biology has been investigated by von Faber (1912), who describes in great detail the development and cytology of a number of species and especially of *C. liberica,* and by de Haan (1923), who concerned himself with *C. robusta.* According to the former, dehiscence of pollen takes place in *C. liberica* in the bud some hours before these open, but, in spite of this, self-fertilization does not always occur owing to the differential rate of growth of the pollen tube when pollen from other sources is present. He found fertilization completed in three to four days with foreign pollen, while five to six days were required in the case of pollen derived from the same flower. The flower is, further, visited by

numerous insects, and the variability of *C. liberica* appears to be due to the frequency of cross-pollination. In *C. Laurentii* and *C. robusta* the behaviour is similar, but is complicated by differences in length of style amounting almost to heterostyly. According to the latter, pollination in *C. robusta* is largely effected by wind. von Faber has shown further that pollen retains its viability for several days, but that it is also very susceptible to changes of humidity, and he suggests that the sterility so common in *C. arabica* is the result of excessive moisture. de Haan goes further and suggests planting up early-, medium- or late-flowering stocks with the object of ensuring the coincidence of flowering with the seasonal occurrence of atmospheric conditions favourable to fertilization.

The development of the coffee industry, especially in the East, has been dominated by the question of disease. In 1876, after the outbreak of *Hemileia*, *C. liberica* was introduced into Java and later, in 1900, *C. canephora*, and in most countries several species of coffee are under cultivation. The earlier work on coffee was confined to the trial of the comparatively large number of specific forms available, combined with the propagation of any variant forms that happened to be identified and appeared to possess characters of economic value. In some cases these forms have a mutational origin, as is the case with the *Maragogipe* and *Amarillo* coffees of Brazil and the varietal forms *monosperma*, *angustifolia* and *rotundifolia* of Java. In other cases, the selected plant is of hybrid origin and requires to be propagated vegetatively. More recently the work of breeding improved stock has been systematically undertaken in Java, and an account of this work has appeared in a series of reports of which the fifth, and latest, is by Lambers (1931).

As in other plantation crops, the value of a particular variety is dependent on two factors, yield and quality of product. Of the factors controlling the latter, little definite is known. To a large extent quality is characteristic of the species or variety, but it is additionally affected by the process of curing, or removing the pulp, subsequent drying of the seed and removal of the parchment-like endocarp. Of major importance is yield, and attention has

been directed mainly to securing regular and high yield. Closely associated with the question of yield is that of disease. Inter-specific crosses have been made by Cramer with varying success. The F_1 of *C. liberica* × *C. arabica* yields a plant very resistant to *Hemileia*, but is a low yielder and often sterile. *C. robusta* × *C. arabica*, however, yields well. *C. congensis* is another species which seems likely to yield hybrids of value and is being tested both in Java and Porto Rico (McClelland, 1924). Recent work in the East has been described by Hille Ris Lambers (1929), who notes as characteristic of the coffees a dominance of maternal characters. At the present time much remains to be learned about inter-specific fertility and the cytology of inter-specific crosses. Of *C. liberica* alone does the chromosomal number appear to have been determined by von Faber (1912) at $N = 8$.

That the coffee plant is readily propagated vegetatively has long been known and propagation by such means has been practised for many years in the Dutch East Indies. The first attempts at grafting belong to last century and were directed to specific objects. *C. arabica* was grafted on to *C. liberica* stock as being more resistant to attack from eelworm, while grafting was also employed to propagate chance hybrids showing desirable characters. An account of these early experiences is given by Cramer (1924). With the co-ordination of the work of breeding more valuable types, the systematization of the practice of grafting has assumed greater importance, and it may be noted that, owing to the dimorphic nature of the branching system, it is of importance to select only vertical shoots for grafting. At the present time the general introduction of grafting into field practice has not been adopted; the function of the graft is to serve as a rapid test of the desirability of the mother tree. Any selected tree is simultaneously tested through its vegetative, grafted, and its seedling, offspring. By the time the seedling offspring have demonstrated the capacity of the mother plant to hand on its desirable characters, the grafted plants will be yielding and, if planted in a compact area, will provide from the inner trees a supply of seed which will have arisen as the result of self-fertilization. Self-fertilization may be assured also by forcing the plant

to flower by irrigation during the resting season. Little information is available as to the most suitable stock, which probably will be found to differ for different conditions. Hille Ris Lambers notes that Cramer has selected a true *robusta* × *Quillou* hybrid as standard stock for the local conditions. With the range of species and varieties now available, the possibility of securing a plant adapted to local conditions lying within the general range of coffee culture is a matter to which experiment can now provide a solution.

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CACAO (*THEOBROMA CACAO* L.)

The " bean " from which the cocoa of commerce is derived is the seed of the Sterculiaceous plant, *Theobroma cacao* L. The home of the genus *Theobroma* appears to be the Amazon and Orinoco valleys, from which the economic forms have been carried throughout the northern stretches of South America, Central America and the West Indian Islands, throughout which area it is doubtfully indigenous. This doubt is due to the fact that the plant had long been in cultivation when America was first discovered, a cultivation of a primitive kind readily reverting to wild growth. As is usual in such cases, the exact origin and even the specific limits are doubtful. Pittier (1930) has given a classification determining nineteen species. A considerable literature exists on the question of the origin of the economic species and the original habitat of these and the subject has been recently discussed by

Myers (1930), but even old plantations, such as that described by Dash (1929), contain a very diverse series of types.

Interest centres on a single species *T. cacao* L.; for though a second species *T. pentagona*, Bern., sometimes classed as a variety of *T. cacao*, is cultivated in Central America, it is of small economic importance. From America the cultivation has spread to all the countries of the world where the climatic conditions are favourable. These include the moister tropical areas where conditions approximate to those of a tropical rains forest. The more important extra-American countries are Ceylon, Java and West Africa, especially the Gold Coast, where the development since the 'nineties has been phenomenal. In conformity with its natural habitat the crop is usually grown under shade, though sometimes, as in Grenada, shade is not used.

The cacao plant is a small spreading tree attaining a height of 20 to 30 feet and, in exceptional cases, even more. The habit of growth is peculiar and important. The main axis terminates in three to five spreading branches, the jorquette, from below, and through which a vigorous shoot, the water shoot, grows to continue the vertical development of the plant. This water shoot, in turn, produces a similar whorl of branches, so that a typical tree consists of a series of superimposed storeys. The inflorescence is a dichasial cyme, much condensed to appear as clusters borne on cushions situated on the trunk and branches. The five stamens, each bearing four anthers and alternating with an equal number of staminodes, are recurved so that the anthers lie in the cup-shaped bases of the petals. The fruit is a large berry containing numerous exalbuminous seeds embedded in a mucilaginous pulp.

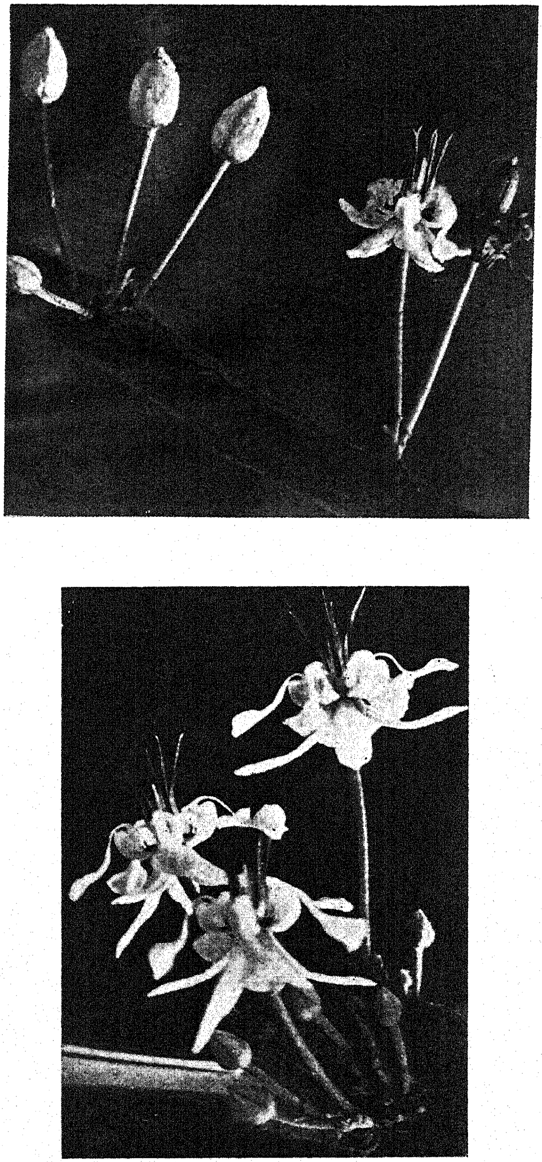
The crop as grown consists of a vast assemblage of different types and, as is usual with economic plants, it is the organ of economic importance, in this case the fruit, which forms the basis of the attempts to classify these types. These are discussed in great detail by van Hall (1914),[1] who distinguishes two main types, *Criollo* and *Forastero*. The former is characterized by the comparatively soft fruit wall and the rounded seeds of a white or pale violet colour; the fruits of the latter are somewhat larger

[1] The latest edition of this work is quoted in the references to literature.

with a hard, often warty and basally constricted, fruit and flattened seeds of a deep colour. Associated with these differences are certain vegetative characteristics which may be summed up as a greater vegetative vigour in the *Forastero* type. Of these two types the *Criollo* is the least variable; the *Forastero* type exhibits a wide range which in plantation parlance is covered by the terms *Angoleta*, *Cundeamor*, *Amelonado* and *Calabacillo*. Pittier (1925) has considered the differences between the two forms as of sufficient importance to justify specific definition; *Forastero*, of which *Calabacillo* is taken as the type, he terms *T. leiocarpa*, Bern., leaving *Criollo* as the typical *T. cacao* L. In the suggestion of a dual origin geographically delimited he is probably correct, but the specific distinction hardly holds as a satisfactory classification of the cultivated crop. Harland (1925a) has drawn attention to the fact that in Trinidad the trees form a set of extremely complex hybrids, while in Ceylon van Buuren (1928), in an analysis of the progeny of a single tree of "good Forastero strain," found all forms from *Criollo* to *Calabacillo*, and he sums up the position by the statement that nearly every tree can be described as a form. There can be little doubt that Cheesman is correct in writing (in a personal communication) that the crop may be considered as a vast F_n between *Criollo* and *Calabacillo*.

Under these circumstances attention has naturally been directed to a study of the biology of the flower and to the methods of fertilization. Harland (1925b) has studied the method of fertilization in Trinidad and summarizes earlier observations. He confirms the general opinion that the main agents of pollination are ants and aphides, but he notes that some flying agent is also at work. He concludes that the majority of flowers pass through their life history without adequate pollination. Stahel (1928) has studied the opening of the flower and anthesis in great detail. The flower opens from 5 p.m. onwards; pollen is shed between 4 a.m. and 5.30 a.m., while the stigma is receptive from 5 a.m. to sunset. His observations on the agents of pollination confirm earlier conclusions. Of interest in this connection is the evidence drawn from the so-called "male cacao" known to all planters as trees which flower abundantly but set no fruit. Harland found in

PLATE VII



Theobroma cacao L.

After Stahel. *Reproduced from " Verh. Akad. Wet.," Amsterdam.*

[*To face p.* 174.

one of these trees that pollen was never formed, and yet nine flowers out of one hundred examined bore pollen on the styles. There is here sufficient evidence that cross-fertilization takes place to an extent which will account for the observed heterogeneity of the crop. Linked with these observations is the cytological work of Heyn (1930) on the reproductive organs in which he reviews the earlier work of Kuyper (1914), who determined the chromosome number at N = 8, and Cheesman (1927).

Considerable differences exist in the value of different classes of commercial cacao and market value is very largely determined by country of origin. Behind this superficial distinction lie more solid grounds for the discrimination shown. The cacao of commerce is not usually the bean simply dried. The ripe fruit on gathering is split open and the seed with the surrounding pulp submitted to a fermentative process which affects not only the pulp but the bean itself. The chemical changes which accompany the fermentative process are not fully understood, but largely influence quality. Direct fermentative action appears to be limited to the pulp, but the heat thereby developed is sufficient to kill the embryo, permitting diffusion of, and interaction between, the cellular contents. To a very large extent, therefore, quality is a controllable character not inherent in the plant, and where cacao is prepared, as it is in the Gold Coast, in small quantities by unskilled hands, the low quality associated with those countries is primarily due to faulty preparation. There is, however, a definite, but ill-determined, source of quality which is inherent in the plant, and the fact that quality is to some extent associated with the name of those countries in which *Criollo* is grown indicates that the superiority is inherent in this form. This somewhat indefinite knowledge and the question of its association with particular types has been discussed by Watts (1925).

In the absence of any very definite guide as to a basis for selection for quality, work on the plant itself has been directed mainly to the question of yield. The conditioning factor in these investigations is the smallness of the number of fruits which mature relative to the number of flowers produced. Stahel (1928) calculated that a nine-year-old tree studied by him produced some

50,000 flowers of which some 3,000, or 6 per cent., set, while of these only 100 reached maturity. Similarly Hewison (1930) found 98 to 99 per cent. of the flowers to open failed to reach maturity. He found, further, that the loss is not due to a single cause, for, while the major loss occurs during the first week after flowering, a further appreciable loss occurs between the third and seventh week. This observed loss is greater than the lack of adequate pollination noted by Harland can explain. Hewison's observations indicate a subtle interrelation between environmental conditions and setting which require further elucidation. Particularly he notes the interdependence between number of fruits setting and number already set. Though the cacao plant shows a definite seasonal response in the matter of flowering, there is practically no season in which flowers and fruits are not borne, and Cheesman (1927) notes the similarity here to the phenomenon of boll-shedding in cotton and considers it to be conditioned by nutrition.

It is clear from this work that the actual number of flowers produced is of small importance in the determination of yield; the important question is the number of fruits which pass the critical first eight weeks of the twenty-four which elapse between flowering and maturation of the fruit. In this matter there is a wide range between different trees. At one extreme lie the " male cacao " trees to which reference has been made, which set no fruit; at the other, plants which produce up to 400 fruits per annum. van Hall (1930) records that anything from 30 to 50 per cent. of the trees of an ordinary estate yield not more than 1 lb. cacao per annum and another 20 per cent. below 2 lbs. Similar results have been obtained by Auchinleck (1928), who has recorded the yield of a large number of individual trees. The determination of intrinsic capacity to yield offers considerable difficulty. Apart from local influences which will favour one tree as against another, cultural methods will affect yield. Pruning, especially in as far as it concerns the cutting of water shoots, materially affects the shape of the tree, but little is known as to its effect on yield, which probably varies with the particular environmental conditions. Shade, again, has a material effect on yield, and here again the

amount of shade desirable is probably a function of the local conditions. In Grenada cacao is normally grown without shade. In Trinidad Freeman (1929) has shown that light shade gives the best results, but it has to be shown that this is more than a local effect limited to the particular estate. Yet again distance of planting has a considerable effect on yield which is closely connected with age. In Trinidad observations recorded by Freeman (1929) show small differences in yield per tree up to the tenth year, but subsequently wide planting is associated with higher yields, those at 18 × 18 feet at fifteen years producing approximately double the yield of those planted at 12 × 12 feet. On the same Trinidad estate manuring produced little effect, again probably a local effect, but trenching between the rows about every fifth year was markedly beneficial. These are all factors which must be taken into consideration and standardized before the intrinsic value of a tree as a heavy yielder can be determined.

Nevertheless, when due allowance is made for all these adventitious factors which affect yield, there remains a large residuum which must be attributed to the inherent capacity of the plant, and the question arises whether this capacity is heritable. Since, too, cacao is readily propagated vegetatively by budding, the further question arises as to whether yield is handed on to the vegetative offspring. Here a further point arises. Mention has been made of the dimorphic character of the shoots ; the laterals arising from the jorquette and the water shoots. Harland (1924) has shown that the type of tree, and probably in consequence the yield, is materially affected according as the bud is taken from a lateral or from a water shoot. Freeman (1928) has described a series of records of groups, of twenty trees each, derived from twenty-eight selected trees, ten of each group being seedlings and ten budded. The results of the first ten yield-years have been analyzed by Harland (1928), and he found that, among the first seven best budded strains, four occurred in each series with an average for the period of 189 to 186 pods per tree, while, among the worst eight strains, two occurred in each series each with an average of forty-two pods per tree. Similarly, among the seven best seedling strains, two occurred in each series with an average

yield for the period of 220 to 215 pods per tree. It is noteworthy that the two best seedling strains differ from the four best budded strains. Harland concludes that high yield is not necessarily handed on either by budding or through the seed and that it is possible to determine the inherent capacity of a tree only by actual determination on the budded or seedling offspring. Nevertheless, the discovery of differences of the magnitude here indicated, equivalent to an increase of 60 per cent., among so small a number (twenty-eight) of parent trees offers a promise of still better results with an extended application of the test to recognized high yielders. Even among the strains here noted the yield per tree ranged from under 50 to 550 among the budded plants, while among the seedling plants one tree yielded over 700 fruits.

Work along somewhat similar lines has been pursued in Java since 1912 and has been reviewed by van Hall (1930), who, in a second communication (1931), deals with its bearing on the practical problems arising out of the revived interest in cacao which originates in the setback to rubber. The material on which this work is based was composed of the progeny of a few *Forastero* trees, accidentally introduced from Venezuela, which proved to be hybrids between *Criollo* and *Forastero*, the former of which alone had, up to that time, been cultivated in Java. Budded and seedling offspring from twenty-four mother trees were intensively studied and the results are comparable with those obtained in Trinidad ; but van Hall points out that, though the average yield of both budded and seedling offspring is less than that of the respective mother plants, as a general rule, though not always, the heavy-yielding mother produces heavy-yielding offspring and there is a definite correlation between mother trees and both budded and seedling offspring. This conclusion has the very practical bearing that, by making use of the offspring, whether budded or seedling, of heavy-yielding mother plants, a very definite increase of yield will be obtained. Cohen Stuart (1931) has described the plan of propagation now adopted in Java. He confirms the above observation that progenies on the whole are parallel with the parent trees, and he calculates that, from the trees forming the highest 4 per cent., a yield 5·64 times the average

is obtainable. More recently Cohen Stuart and Haan (1931) have given a very detailed account of later work in Java. In addition to describing the experimental work, they show that on plantations trees yielding below 100 pods supply 18·8 per cent. of the crop only, and they consider that the removal of these would actually increase the crop of the following year owing to increased yield from border trees; but they suggest that, in practice, the removal should be gradual.

Few observations have been made with respect to the mode of inheritance of those characters which affect the quality of the product. Wellensiek (1931) considers the white cotyledon colour to be associated with quality and to be a simple recessive; he therefore considers it possible to combine the good qualities of the *Criollo* and *Forastero* types by hybridization.

It has been customary, as in the Trinidad work, to measure productivity by the number of pods yielded per tree, but large differences are found in the weight of cacao obtained from individual fruits. It is a point of considerable importance which has been studied by Cohen Stuart and Haan (1928). As an example of the magnitude of the difference, they note that the strain 11, the highest yielder, gave an average of 3,550 g. per tree from 77·4 fruits, while strain 36 gave an average of only 3,120 g. from 100·7 fruits.

In addition to differences of yield, the Java strains exhibited varying, but marked, degrees of resistance to disease, particularly to *Acrocercops cramerella*, the cacao moth, and to *Helopeltis*.

Note.—Since this article was written there has appeared an excellent review of the available knowledge concerning cacao by Cheesman (The Economic Botany of Cacao, Suppt. to *Trop. Agric.*, June, 1932).

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TEA (*CAMELLIA THEA* LINK.)

The economic use to which tea is put is too well known to merit description. The plant belongs to the natural order *Theaceæ* and is a native of the Far East. Tea has been grown in China from the earliest days, but the main supply of tea in commerce comes from India, Ceylon and Java, where the industry is of comparatively recent origin. The problems of the industry will be understood most readily from the history of its establishment in these countries. Tea was first introduced into India in 1834 and, during the early years, cultivation was limited to the plant, derived from seed introduced from China, to which centuries of cultivation had imparted definite characteristics. Though the existence of the tea plant growing wild in Assam and Manipur was known before that date, the value of the local plant was not recognized. This recognition came later and, in consequence, the first plantings of the indigenous stock were made among areas in which the Chinese

variety was established. Since, as will be shown below, the plant is self-sterile, the subsequent plantings derived from plantation seed consisted of an intense mixture of hybrid plants. In Ceylon tea cultivation followed the collapse of the coffee industry in the 'seventies as the result of the outbreak of *Hemileia*. The seed used for its establishment came from Assam, and here, too, a hybrid crop is grown. The Javan industry started independently in 1826 with seed imported from China, but in 1878 seed was imported from Assam, with the consequence that here, too, a hybrid crop is grown. Details of the introduction into India are to be found in Watt (1908).

In this admixture of the plantation crop it is of little value to attempt classification; it is only possible to indicate the major varieties known to grow wild which have entered into the composition of the present crop. As is usual in cultivated plants, these varieties are defined largely by the characters of those structures which bear on the economic value of the plant. Cohen Stuart (1920) has recognized four groups :—

(1) Dwarf habit; leaves small, 4 to 7 cm. long, with 6 to 8 pairs of veins. East and south-east China.

(2) Height up to 5 m.; leaves up to 14 cm. long, with 8 to 9 pairs of veins. Hupeh, Szechuan and Yunnan. = *v. macrophylla* Siebold.

(3) Small tree 5 to 10 m. tall; leaves up to 17 cm. long, with 10 pairs of veins and light green in colour. It is the "Shan" form and includes the "Assam" teas. The Shan States.

(4) Tree up to 20 m. tall; leaves 20, 30 or even 35 cm. long, with 12 to 15 pairs of veins. It is the "Manipur" tea from Manipur, Cachar and Luchai.

The flower is hermaphrodite and remains open for some three days. Though the pollen is shed with the opening of the flower and the stigma is at the same time receptive, Cohen Stuart (1916), who has studied the flower of the tea plant in all its aspects, failed to obtain a single case of self-fertilization, and the plant appears to be completely allogamous, a result which must be compared with the recent work of Bachtadze (1931), who claims to have secured seed from protected plants. In his paper Cohen

Stuart described the development of the generative organs and attempted to trace the cause of the sterility. He notes the slow growth of the pollen tubes, leading to fertilization only after some seventeen to nineteen days, a considerable irregularity in the number of megaspores found and a delay in the development of the embryo. The haploid chromosome number he places at 15.

The present position of the tea industry is, thus, that the crop consists of an intense mixture of heterozygous plants, any attempt to introduce purity into which by the direct method of purification is practically impossible. Vegetative reproduction, which had been studied by Keuchenius (1923), has, according to Macmillan (1925), proved impractical as a plantation practice, though Cohen Stuart (1930a) has obtained a greater amount of success and contemplates the extended use of grafted plants.

A further difficulty lies in the fact that no definite knowledge exists as to the factors on which quality depends. Quality results in the first place from the age of the leaf plucked, in the second, on the preparatory processes which include fermentative activity, and is judged by the empirical process of tasting. The problem of tracing back quality to a character, or group of characters, inherent in the plant, and sufficiently definite to form the basis of breeding, is hardly capable of solution. Nevertheless, efforts in this direction have been made by Gogh (Cohen Stuart, 1930a), who found differences in quality between pluckings of single trees of a magnitude which could be identified by expert tasters.

The main objective of the breeding work which has been undertaken has, in consequence, been limited to productivity. For a number of years an investigation has been carried on by Cohen Stuart (1929, 1930a) into this matter. Considerable practical difficulty occurred in the determination owing to the varying sizes of the bushes. In the determination of productivity he adopts a *productive index* which is the *yield intensity* of the individual plant relative to the *yield intensity* of the whole garden, *yield intensity* being defined in grammes per sq. metre pruned surface. By these criteria he has selected a number of plants of high productivity which he then treats as follows :—

From each of these plants a certain number of grafts are made,

some of which are planted in an isolated garden, similar control gardens being planted up with grafts from medium and bad yielders, while other grafts, at least four in number, are planted promiscuously in a test-plucking garden. Further, he establishes a series of small isolated gardens containing eight grafts of two selected high-yielding plants. The objective is to obtain a progeny uniform both in type and superiority of yield, and, from the two plants forming a combination approximating to this result, large seed gardens for the extensive production of seed will be established with grafts. With a plant so slow to reach maturity as is tea, the work must be necessarily slow in yielding results.

In a further paper Cohen Stuart (1930b) develops a method of nursery selection. The plants in the nursery are cut at 25 cm. and, at six-monthly intervals, at 30 cm. and 35 cm. From the figures of foliage production he obtains a measure of vigour which he has reason to suppose corresponds to yield capacity. The method is still in the experimental stage for, if variation due to age be removed, border effects are introduced which may have an equally disturbing influence.

The possibilities of improvement by these methods are hardly yet apparent, but Gogh (1931), in a description of a series of experiments having as their aim in one case yield and in another quality and using vegetative propagation, obtained a yield of dry tea per hectare as much as ten times the normal yield.

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CHAPTER X

SUGAR

SUGAR CANE (*SACCHARUM OFFIKINARUM* L.)

THAT present-day essential commodity, sugar, is derived from a number of widely different plants, members of divergent natural orders. Of these, the sugar cane, *Saccarum officinarum* L., belonging to the *Gramineæ*, and the sugar beet, *Beta vulgaris* L., belonging to the *Chenopodiaceæ*, are of outstanding importance. In the early days, until, as the result of Napoleonic effort, a beet industry became established on the Continent early in the nineteenth century, the cane plant was the source of the commercial supplies of sugar. At the present day some 25 million tons of sugar are produced annually, of which some 15 million tons are derived from cane. This position is largely the outcome of the recent war, which was responsible for a great contraction of the Continental beet industry. By 1884 production of sugar from beet had caught up the production from cane, each producing some $2\frac{1}{2}$ million tons, and this lead was maintained until, as the result of the Cuban war and the subsequent reorganization of the industry in that country and Porto Rico, cane production again took the lead.

The sugar cane is essentially a tropical plant requiring high temperature and plenty of water. Its home is in the tropics, though it is found growing outside the limits of the tropical zone, notably in northern India, one of the major areas of sugar production, Egypt, Natal, Louisiana, the Argentine and northern New South Wales. It is also grown to a small extent in southern Europe (Spain), China and Japan. Given the necessary humidity it is capable of growing at considerable altitudes, as in Uganda. The plant is propagated vegetatively and, consequently, the varieties of cultivation are, at least in the case of those varieties of which the origin is known, actually the product of a single

plant. The cane itself consists of a series of nodes, separated by internodes each carrying an eye, or bud, and a band from which adventitious roots develop. This cane is cut into sections each containing one, or more, nodes and, on planting these sections, the eye develops into a shoot the lower internodes of which are compressed. The eyes of these lower nodes develop into secondary shoots, which, in their turn, give off further shoots, so that the developed plant, or stool, consists of a group of canes. From the root bands of the lower nodes both of the primary, and later, shoots, adventitious roots develop which replace those arising from the parent section. Considerable varietal differences exist in the number of shoots arising in a single stool and in the character of the root system, these differences being of considerable importance inasmuch as the former has a direct bearing on yield and the latter on drought resistance and adaptation to soil conditions generally. Partly owing to the difficulties inherent in the study of an organ which cannot be directly observed under conditions of normal growth without disturbing the plant, and partly owing to the capacity of adaptation to varying soil conditions which most roots exhibit, a capacity which makes it a matter of extreme difficulty to determine the potentialities inherent in the plant, root development has rarely received the attention it deserves. In cane it has an added importance owing to the wide range of conditions under which the crop is grown, and especially when, as in northern India, the plant has to establish itself under conditions of intense drought. Lee (1926) has made an extensive study of the root system of the cane plant, while in continuation of Barber's earlier work on the subject, the commencement of a systematic study with a view to determining the intrinsic varietal characters has been made by Venkatraman (1929) at Coimbatore.

The value of the cane plant lies in the sucrose which is contained in the parenchymatous tissue of the stem. The sugar is extracted by a process of crushing the cut cane after it has been stripped of its leaves, clarification of the extracted juice and subsequent concentration until crystallization occurs. In the simpler processes concentration takes place in open pans and a crude product obtained, the *gur* of India and *muscovado sugar* of the West

Indies. In modern practice sugar is obtained in a high degree of purity by a complex process conducted under strict chemical control at all stages. The unit of modern manufacture is large and involves the expenditure of a considerable volume of capital. High efficiency in such a unit is essential to success and makes many demands on the cane grower. Among these points are a low percentage of fibre and a high percentage of sucrose, which latter must be not only absolute but relative to other (reducing) sugars present; for efficiency of extraction, the extent to which the sucrose present is recovered, depends in large measure on the amount of reducing sugars in the juice. The relative amounts of sucrose and reducing sugars in the plant vary considerably at different stages of growth. In most cane-growing countries climatic conditions, the incidence of a dry season, a relatively cold season or both in association, differentiate a period of low growth activity and, with the incidence of such a season, the sucrose content increases while the amount of reducing sugars diminishes. When the sucrose content is at its maximum the canes are said to be ripe; their condition is then the optimum from the aspect of the factory. After a certain period a reversal of the process takes place and the canes become over-ripe. Over-ripeness is a condition usually associated with a renewal of growth, which, again, is associated with climatic conditions. Different varieties show a wide range of variation in the date of maturation, and, with the increased size of the modern unit involving large fixed overhead charges, this has become a matter of considerable importance. Under these conditions, economy is closely bound up with the length of the working season and the factory will be best served by a well-managed estate growing a series of varieties having successive maturation dates. Modern practice aims, therefore, at providing for each locality a series of suitable varieties to be grown in such relative proportions that the factory will be fed with mature canes for the longest period of time.

Considerable controversy has ranged round the classification of the canes which as yet awaits final solution. The problem is complicated by the fact that the true canes, *S. officinarum* L., cross readily with the wild species *S. spontaneum* and yield

offspring which would undoubtedly be classified as *S. officinarum* were their history not known. In fact, *S. spontaneum* forms one of the parents of many of the canes introduced into cultivation in recent years both from the breeding stations of Coimbatore in India and of Java. Even the specific limits, therefore, are ill-defined. More recently still, Venkatraman (1930) has succeeded in obtaining crosses between one of the P.O.J. series of canes of Java having *Noble* and *S. spontaneum* blood in its parentage, and an early maturing *Sorghum*. *S. spontaneum* L. is a very variable wild species widely distributed throughout the East and, in some of its many forms, contains a considerable amount of sucrose in the stem. In one form it is the noxious weed of northern India, there known as *Kans*, in another it is the *Glagah* of Java. Opinion is hardening to the view that the canes of cultivation have a dual origin; one, that of the so-called *Noble* canes, lying in Oceania and possibly in New Guinea, while the other, that of the Indian canes, lies in the neighbourhood of the head of the Bay of Bengal. The parental type, the wild form, from which the *Noble* canes have been derived, is yet to be discovered, but the Indian forms appear to be definitely derived from *S. spontaneum*. Barber, in his monumental work on the Indian forms (1915, 1918), from a study of the morphology of the plant, recognizes five groups of Indian canes, *Saretha*, containing the well-known forms *Saretha* and *Chunnee*, *Sunnabile*, *Pansahi*, containing the widely grown *Uba*, *Nargori* and *Mungo*; and he summarizes his conclusions (1928) with the suggestion that the first, and possibly the second, are directly derived from *S. spontaneum*, while the latter three groups may be derived from a cross between one of the earlier forms and a thick, or *Noble*, cane. This conclusion of Barber's is supported by Deer (1929, 1930). Jesweit in conjunction with Backer has made an extensive study of the *Noble* canes in Java and their results are recorded in a series of papers, published during the last fifteen years, in the *Med. v. L. Prœfsta. v. d. Java Suiker Industrie*; and the former has attempted a classification of the genus *Saccharum* based on the distribution of hairs in the inflorescence. He suggests four species:—

Main axis of the inflorescence carrying long hairs—

S. spontaneum. Lodicules ciliate ; the wild form.

S. sinense. Lodicules non-ciliate ; leaves broad. Barber's three groups, *Pansahi, Nargori* and *Mungo* with *Uba* as a widely grown representative.

S. barberi. Lodicules non-ciliate ; leaves narrow. Barber's two groups, *Saretha* and *Sunnabile.*

Main axis of the inflorescence without hairs—

S. officinarum. Subdivided according to the presence or absence of the fourth glume. The *Noble* canes.

Further light has been thrown on the subject by Bremer, who has approached it from a cytological aspect. His original contribution (1922) has been supplemented by further contributions (1924–1931) dealing with the cytology of the *Noble* canes, *S. spontaneum* and many of the crosses arising therefrom. The story is as yet far from complete, but the work indicates that in the genus *Saccharum* the number of chromosomes in general agrees with the basic number found in the *Andropogoneæ,* namely ten. In *S. officinarum* (Jesweit's definition) the number is forty haploid ; in *Glagah,* the Javan variety of *S. spontaneum,* the number was found to be fifty-six, but in a slightly different form from Celebes the number was found to be forty. It appears, therefore, that *S. spontaneum* is itself a composite form and requires closer study than has yet been given to it in view of the use now being made of *S. spontaneum* in the production of commercial canes.

Of especial interest is his investigation of *Kassoer,* a local cane used in Java as a parent in some of the earlier crosses in place of *Chunnee* originally used. The number of chromosomes found in it was 136, which he interprets as 80 + 56, the diploid number of the *Noble* canes combined with the haploid number of *Glagah.* It would appear that, at some stage of division, the chromosome number of the *Noble* cane is, in such crosses, duplicated, and the conclusion can be reasonably drawn that *Kassoer* itself is the product of a natural cross between *Glagah* and *Black Cheribon,* the only cane commonly grown in Java prior to 1900. This work has thrown further light on other cases. *Toledo,* a Philippine cane supposed to be a natural cross between *S. spontaneum* and *S. officinarum,* was found to have a chromosome number of 120,

which can be interpreted as 80 + 40, the duplicated number of a *Noble* cane with a form of *S. spontaneum* having 40 chromosomes. Again, *Tanannge,* a cane obtained from Celebes and Borneo and placed in the *Kassoer* group, was found to have 30 chromosomes haploid, and it is, therefore, distinct from *Kassoer.* There can be little doubt that an extension of cytological work to other groups will throw much light on the origin of the various canes; especially does it offer a means of testing the suggested dual origin of the Indian canes to which reference has been made above. Equally, it will undoubtedly facilitate the selection of those varieties which will offer the greatest promise of parental value. In his latest paper (1931b) Bremer has given the results of his cytological investigations in a number of Indian canes. From these results, based largely on somatic determinations made in the absence of floral material, he concludes that Barber's classification of these canes stands in need of revision.

Not the least of the difficulties encountered in the varietal study of the cane plant arises from its extended distribution and the confusion in terminology which has arisen therefrom. As one striking example may be noted the case of that undoubtedly Indian cane, *Uba,* grown so extensively in South Africa. Hill (1931) adduces evidence to show that the name *Uba* arose in that country from the only three letters legible on the consignment label which were three letters of the word Durban, the port of consignment. It is a cane definitely distinct from the *Uba* of South America, which is derived from the local word meaning "reed."

The inflorescence of the sugar cane is an open, much-branched, panicle, known as the arrow. Each rachis is articulate and very brittle; at each node there are two spikelets, alternately placed, one of which is sessile and the other stalked. At the base of each spikelet there is in certain varieties a tuft of long hairs which forms a character used for classificatory purposes by Jesweit, and each spikelet carries a single flower. Typically, each flower is subtended by two bracts, respectively the inner and outer glume. Within these two glumes lies a third glume, the sterile lemma; sometimes a fourth glume, the fertile lemma, and a

fertile palea. Within the glumes also lie two lodicules, a whorl of three stamens and the ovary with two plumose styles.

Propagation of the cane being vegetative, all questions of gametic purity and its maintenance are removed from the field of commercial cane growing. The importance of seed production is, however, in no way diminished on this account, though delicacy of manipulation has limited the production of seedlings, especially where a knowledge of paternal as well as maternal origin is required, to stations technically equipped. The simplest method of effecting cross-fertilization is to grow the two parental types in parallel rows and to enclose the arrows of both plants, bent over so as to meet each other, in one cage; but this presupposes a clearly defined plan of campaign of crossing which must be laid down at planting time, and an assurance that both varieties will arrow at the same season. The first condition is, perhaps, capable of fulfilment; the second is not, for varieties exhibit a marked difference in the extent to which they develop inflorescences, a result, no doubt, of the years during which they have been subjected to vegetative reproduction and the consequent elimination during that period of a selection in which fertility would play its part. Further, the conditions which induce flowering are still little understood, though a considerable amount of scattered information, such as that collected by Alexander (1923) in Hawaii, is available on the subject.

Such seasonal differences in flowering can, in some plants, be overcome by storing the pollen of the earlier maturing variety, but this is possible to a limited extent only in the case of cane, for pollen normally retains its viability for a few hours only. Observations on the viability of pollen are numerous, for they have an important bearing on another aspect which will be referred to later; but the most detailed study which has a bearing on the present subject is that of Dutt (1928a, 1929). Dutt succeeded in prolonging the life of the pollen grain to twelve days by storing it in an atmosphere of CO_2 with a relative humidity of 85 per cent. and a low temperature (5° to 13° C.). As a practical solution this offered little advantage, since Venkatraman (1922) had already succeeded in securing a delay of ten days by the

somewhat different method of delaying dehiscence of the anthers. The practical problem of securing cross-fertilization between two varieties having different flowering periods by retention of the viability of the pollen of the earlier variety, therefore, still awaits solution.

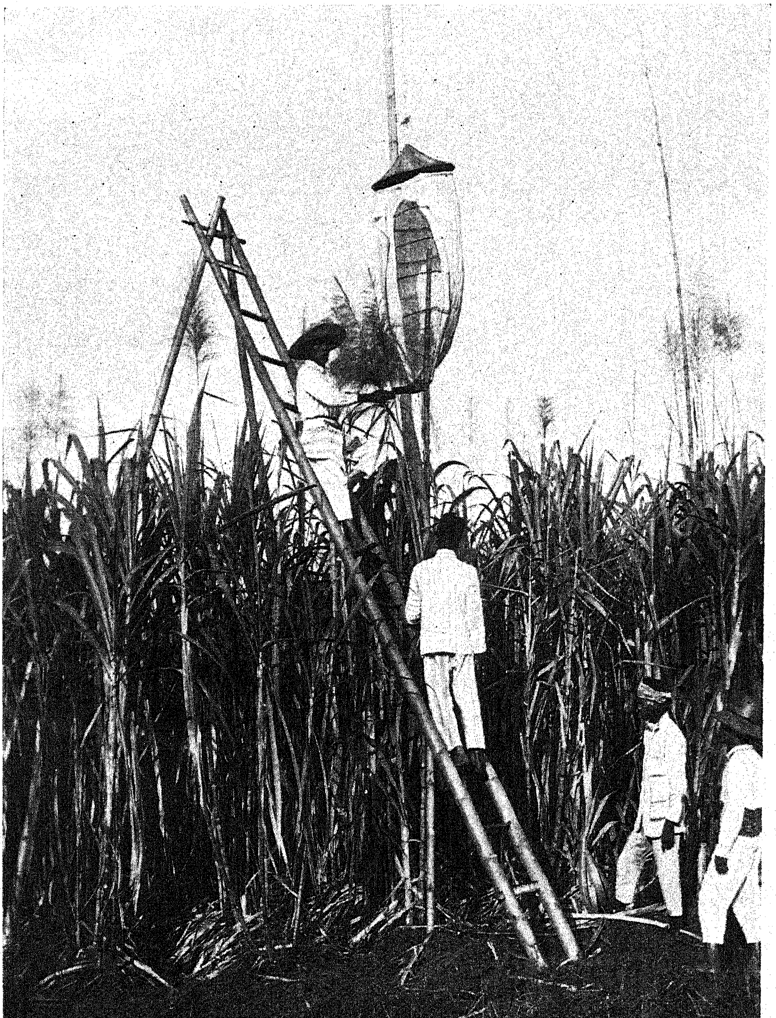
The problem raised by this difference in the arrowing period of different varieties has, however, been partially overcome in another manner. The effect of climate on the length of the growing period is such that practical account has to be taken of it in cultivation. Thus, in Natal, with its distance from the equator and its temperature and rainfall erring on the low side, growth is slowed down to yield a crop once only in two years. At the other extreme, in northern India, the high temperature of the monsoon period leads to a growth which yields a crop every year, actually with ten to twelve months between planting and harvest, in spite of the fact that a period of low temperatures followed by a period of low humidity limits the period of active growth to less than six months. In both these cases the cane grown belongs to the Indian group. In tropical countries, where more equable conditions both of temperature and humidity exist, *Noble* canes are grown and ripen, in the sense of developing the maximum sucrose content, according to season, but mature, in the sense of flowering, only after a certain minimum period of vegetative growth; and, as these two phenomena are closely interrelated, cane which is planted too close to the ripening season will not arrow till a further twelve months has passed. Walter (1910) has pointed out that, in Mauritius, cane planted at sea level requires thirteen months to mature, while in the same island at 1,100 feet elevation it requires twenty-one months. In Java advantage has been taken of the fact that it is possible to pass through widely divergent altitudes in short distances, to establish plantations at varying elevations extending to over 1,000 feet. At the higher altitudes the flowering period is found to be prolonged and the periods of different varieties tend to overlap. Further, it is possible to convey the arrow destined to be used as male parent from one tract to the other.

This necessity for removing the arrow of the pollen parent,

since the plants to be crossed will usually be separated from each other in space, raises practical problems of another nature. The pollen itself, as has been said, remains viable for a few hours only, while the arrow-bearing shoot soon withers after cutting. Where the arrow is used, these must be replaced at intervals throughout the period of five or more days which the arrow of the mother plant takes to complete flowering. This difficulty has been met in Hawaii by a system, described by Verret (1925), in which, with certain due precautions, the cut stem is placed in a 1 : 2,000 freshly prepared solution of sulphurous acid. Pollen from the arrows of these shoots proved to be viable ten days after separation of the shoot which itself remained alive for several weeks. Venkatraman and Thomas (1926) worked along different lines; they found it possible to identify the arrowing cane sufficiently early for the culm to be surrounded over a distance of one or more nodes with earth, kept moistened, for root development to take place from one or more nodes of the culm which had been surrounded by earth so kept moist. The shoot could then be cut below the rooted area giving a rooted arrowing shoot capable of being transferred to any required position.

The details accompanying the phenomena of flowering have been studied in many countries. In Hawaii Barnum (1926) has made a detailed study, while in Barbados recent reports of the Department of Science and Agriculture contain numerous references to observations on the subject. McIntosh (1930) has summarized these observations and finds considerable varietal differences in the details of pollen shedding both in time and amount. The opening of the flower shows a diurnal periodicity, but, as with other graminaceous crops (cf. *Oryza* and *Sorghum*), there is considerable variation both varietal and local. The pistil is protruded between the closed glumes which are later forced apart by the swelling of the lodicules. The opening of the flower takes place during the night and precedes anther dehiscence by some three hours. The glumes remain open for a few hours only and then close. These differences are of considerable practical importance when it is desired to make crosses. Advantage can,

PLATE IX



Saccharum officinarum L. Effecting cross-fertilization.

By courtesy of The Director of Agriculture, Pasoeroean. Reproduced from "Arch. Suikerind. Ned.-Ind."

[*To face p.* 192.

for instance, be taken of the relatively late hour of shedding of *B* 606 to use it as the female parent. The causes underlying the phenomena are not fully understood, but it is suggested that evaporation is probably of greater significance than actual humidity or temperature.

But there is a further aspect of the question of the viability of the pollen which finds its origin in varietal specialization. The extent to which viable pollen is produced varies markedly not only from variety to variety, but from place to place and from season to season. In certain tracts, notably in northern India and in the southern area of the Australian sugar belt, though the canes may arrow, the anthers fail to dehisce; and here the controlling factor is temperature. Seasonal effects, of which the causes are not so clearly defined, are also found, but behind these there lies a capacity, or incapacity, to set fertile pollen which is inherent in the variety and over which the environmental effects are superimposed. Even under favourable environmental conditions the varietal range of this capacity extends from a failure to set any functional pollen, as in *Lahaina* and *Uba*, through all degrees of semi-sterility indicated by varying percentages of non-viable, shrivelled pollen, to the abundance of viable pollen which is typical of *S. spontaneum*. It becomes a matter of supreme importance to determine the degree of this inherent character. In Java the method adopted is based on the iodine test for starch, presence of starch in the pollen grain being taken as indicative of viability. When the percentage of fertile pollen falls below 40 it is considered necessary to take special precautions where the objective is self-fertilization; where, however, cross-fertilization is desired, the direction of the cross will be determined by the relative capacities of the two varieties to set viable pollen, the mother parent being that having the lower percentage of viable pollen. It may, however, be doubted if the iodine test is more than a rough guide to the capacity of pollen to effect fertilization. Various attempts have been made to devise more reliable methods, but cane pollen, like that of so many plants, does not readily germinate on artificial media. Fairly successful results have been obtained from the use of the stigmata of other plants such as

Datura and tobacco. A full reference to these attempts has been given by Dutt (1928a), who has made a detailed investigation of the problem and worked out the conditions necessary for success in germinating cane pollen on artificial media. Weller (1930) has standardized the conditions of pollen germination still further by paying attention to the *p*H value of the medium. He found a *p*H value of 5·2 to be optimum, but attention to humidity (optimum 96 per cent.) and temperature (optimum 23° C.) was also necessary.

Closely associated with this phenomenon of semi-sterility or viability of the pollen is that other phenomenon of self-sterility. This has been studied by Mangelsdorf and Lennox (1929) in Hawaii. These investigators have determined the degree of self-sterility of a number of varieties. But whether this phenomenon is due to incompatibility or to failure of the pollen tube to reach the ovule before the latter withers remains to be determined.

The position with regard to female sterility is very far from clear though in certain varieties, such as *POJ* 36, a cross between *Striped Mexican* and *Chunnee*, both ovules and pollen are sterile. Here again the iodine test has been used, but, as Venkatraman (1925) has shown, the test is far from infallible.

Owing to the heterozygous constitution of all cultivated canes, which is the natural outcome of a selection which does not involve any consideration of purity of stock, itself the outcome of the vegetative method of propagation, the progeny resulting from a cross, as well as from self-fertilization, exhibits a very wide range of form. Practical efforts to secure improved varieties have consequently been confined to extensive methods. Seedling canes have everywhere been raised in very large numbers and, from these, a rigid selection made. If, in the making of these cultures, chance has in the first instance played a leading part, efforts to reduce the part chance plays have not been lacking in success. Close observation has shown that varieties differ materially in the number of valuable offspring to which they give rise and progress in breeding consists very largely in the identification of those varieties which give the largest number of valuable offspring and in the predominant use of these as parents. The

identification of such varieties and their subsequent use now ranks second only to the introduction of some form of *S. spontaneum* into the parentage in the schemes adopted both in Java (Postumus, 1928) and at Coimbatore in India.

Each country has an aspect of the breeding problem peculiar to itself and has made the object of its work the production of canes which best meet its peculiar conditions. In Java, where the breeding of canes has been carried to a very high degree of perfection, the stimulus came from the damage caused by the disease known as *sereh*, which became prominent about 1882 and still lacks full explanation. The primary object was, thus, to secure a disease-resistant cane, and disease resistance still remains a prominent feature of the present work, though all desirable characters, except such as concern ratoon crops which the system of cultivation does not permit, are taken into account. The earlier work prior to 1893 has been described by Kobus (1893) and consisted of raising and testing seedlings obtained from free crossing. In that year definite crossings were made between *Black Cheribon* and *Kassoer*, a cane which, as has been explained, is almost certainly derived from *S. spontaneum*. In 1890 Kobus had visited India in the hopes of finding a cane resistant to *sereh* and, among other Indian canes, took back with him *Chunnee*, one of the *Saretha* group of thin canes. This cane, mainly because of its high resistance to *sereh*, he crossed with the *Noble* canes and thus derived the earlier forms included in the *POJ* series, many of which have spread over the globe. This principle of crossing the thin canes with the thick, *Noble*, canes has been referred to as a process of "ennobling" the former. In 1905 the process was carried a stage further by intercrossing seedling canes derived directly from *Chunnee* and, in this way, a series of derived *Chunnee* canes were obtained, many of which were added to the *POJ* series. In 1911 attention was again directed to *Kassoer* and, in 1917, as the result of Jesweit's conclusion, based on morphological study, that *Kassoer* itself was a chance cross between *Glagah* and a *Noble* cane, *Glagah* itself was crossed with a seedling of *Black Cheribon* × *Fiji*, producing a plant similar in all characters to *Kassoer*. Further work has followed the principle which may be

termed twice, or thrice, ennobling *Kassoer*, and from this work a number of valuable forms, notably *POJ* 2878, have been derived. The same principle of ennobling *S. sinense*, the second group of Indian canes, has been adopted but with limited success. A full detail of the crosses made between 1893 and 1925 has been given by Bannier (1926).

The Indian problem was a very different one. On the one hand, some 75 per cent. of the whole local consumption of sugar in India is in the form of *gur*, and the balance only as white sugar. Of this balance one-seventh to one-tenth is home produced; the remainder is imported from Java. On the other hand, the main sugar tract lies in northern India, outside the tropics, where climatic conditions limit the growing season to some six months and only the rapidly maturing indigenous canes can be extensively grown for sugar production. The *gur* industry, therefore, is an important factor in the sugar problem, and in this the question of sucrose content, so important where the manufacture of white sugar is concerned, is relatively unimportant. But if India is to become self-supporting in the matter of the growing demand for refined sugar, the need is for a cane adapted to the short season of the sugar tract, with a high sucrose content and adequate yield. The problem is largely economic, the organizing of a supply of canes, adequate for the economic running of a central factory, from a host of peasant holdings; it is largely agricultural, the determination of the correct methods of cultivation to ensure yield; but it is even more fundamentally a question of breeding, the production of rapidly maturing canes having a capacity of responding to intensive cultivation not possessed by the indigenous thin canes, and a sucrose content when ripe comparable with that of the *Noble* canes. The problem is further complicated by the fact that, in northern India, though many of the canes arrow, seed is not procurable and the work of raising suitable canes has to be carried out in another tract. In 1912 a cane-breeding station was opened at Coimbatore, and the scheme of work then laid down by Barber has not been materially altered. Barber was the first to recognize the close affinity of *S. spontaneum* with the canes of northern India and to introduce that wild species into the

parentage of cross-bred canes, a work that he carried out at that station. How far he succeeded is shown by the fact that, according to the Indian Tariff Board Report (1931), 877,000 acres are planted with Coimbatore seedling canes and of these acres the United Provinces and Bihar, the main sugar tract, with a total acreage of 1,644,000, grow 700,000. Coimbatore canes, too, have spread to many of the sugar-growing countries throughout the world. The canes of the Coimbatore series which have become most popular are *Co.* 214, *Co.* 210, *Co.* 203 and *Co.* 205, and of these, *Co.* 205 is the product of a direct cross between *S. spontaneum* and a *Noble* cane. Their full history and their characteristics have been described by Venkatraman (1928). Difficulties in the setting of seed similar to those met with in northern India occur in the southern tract of the Australian sugar belt and in Formosa. Crossings for Formosan conditions are now effected in Java from whence the tassels are sent to Formosa for the germination of the seed (Mangelsdorf, 1930).

The breeding of the sugar cane has nowhere been prosecuted with the same continuity and close attention which has been devoted to the subject in Java and at Coimbatore. Though, in most cane-growing countries, seedling canes are now being raised, the system is an extensive one similar to that originally adopted in Barbados by Harrison and Bovell and continued by the former in British Guiana and by the latter in Barbados. To these two belongs the credit of establishing in 1889 the fact that cane sets viable seed, a credit they share with Soltwedel who contemporaneously and independently established the same fact in Java, though numerous references to seedling canes are to be found in earlier literature. The extensive method as applied in these countries consists of raising, either by selfing or crossing *Noble* canes, as many seedlings as possible and applying to these a rigid selection. In Barbados, as in Java, the stimulus came from disease which attacked the *Otaheite* (*Bourbon*) cane, then the common cane of cultivation. In recent years a more intensive system has been developed here with a view to extending the factory season by raising canes which, while agriculturally suited to the conditions, have different maturation periods. For this

purpose greater attention than was previously given is being devoted to the study of the details of fertilization, the varietal differences which occur in this respect and the varietal capacity to yield useful progeny. Especial attention is being given to the correlation of seedling characters with agricultural characters of economic importance for the purpose of saving labour by the early elimination of useless seedlings. Nicholl (1929) describes the same method as being adopted in Hawaii where *Chunnee*, *Uba* and *Kassoer* as well as the *Noble* canes are among the varieties used in crossing.

The work of Coimbatore is, in many ways, peculiar in that its main effort is directed to the production of canes adapted to conditions very different from those of the station itself, conditions, too, which, in certain areas, approximate to the extreme limits of possible cultivation. Very largely the deciding factor is one of root development, but there arise also questions of response to environment as indicated by the growth period of the shoot. Such questions bear on the common observation that the cane shoot hardly lengthens throughout the hot weather however liberally water may be applied by irrigation, but that directly the air humidity rises with the inset of the monsoon current, a very rapid lengthening of the shoot takes place. The importance of such considerations in the selection of canes for particular tracts has been recognized by Khanna and Venkatraman (1930) in breeding for such limiting conditions as exist in the Punjab.

In all this work the practical aspect has been placed severely in the foreground and relatively little attention has been given to any genetical analysis of the plant itself. Apart from the difficulties in such an analysis, several reasons exist for the neglect of a study usually considered to be of fundamental importance. Cane is, in practice, vegetatively reproduced and the varieties, actually single plants, commonly grown are themselves heterzygous with respect to a large number of characters. Further, the question of purity or otherwise of a seedling is a matter lacking practical importance; for a satisfactory cane, once raised, is capable of indefinite vegetative multiplication. Nevertheless, a certain number of observations bearing on this aspect are on record and the lines on which further work is planned have been

laid down by Cheesman (1928). The possibility of its fulfilment depends on the capacity of the plant to survive a long period of inbreeding. The existing varieties of cane may be presumed to be heterotic forms and experience with maize gives some indication of what may occur when a homozygous condition is approached. The occurrence of varying degrees of self-sterility in many of the present varieties and the loss of vigour which so frequently accompanies continued inbreeding throw doubts on the possibility to which practical experience alone will supply the answer.

Some fifteen years ago Barber (1916) attempted to trace correlations between such economic characters as sucrose content and tillering capacity on the one hand and certain morphological characters as leaf measurements on the other. Though his observations were conducted on the mature plant, his objective was the discovery of some character which could be identified in the seedling and used as a means of early elimination of undesirable material. Though he obtained indications of correlation, no correlation coefficients were worked out. Similar work with the same objective has already been noted from Barbados. It has to be recognized that, in a plant like the cane, possessing a large number of chromosomes, the scales are heavily weighted against finding any correlation arising from linkage of characters, while the matter is made even more complicated since, in the absence of any homozygous race, the genetic constitution is far from clear.

Venkatraman (1927), from material supplied by the crosses at Coimbatore, has commenced the difficult study of a preliminary identification of the elementary characters of the plant. Of the more important of such characters he deals with leaf width, leaf-sheath colour, ligular process, circlet of hairs situated on the node, shape of joint, length of internode and ivory markings on the internode. Evidence is drawn both from seedlings resulting from self-fertilization and from cross-fertilization, but as, in the latter case, the parental behaviour is not always recorded, the results are not readily interpreted. Of greater interest are his observations on those more complex characters on which the economic value of the plant depends, such as vigour, habit, tillering capacity, thickness of the cane, quality and quantity of

the juice, root character and susceptibility to Smut. In large measure these observations do little more than confirm what previous experience had indicated, that the inherent capacity of varieties to produce valuable offspring varies considerably. Habit had been studied by Barber and an extension of his work to include the influence of crossing has been recorded by Vital Rao (1920). Tillering, which had also been studied by Barber (1919a), shows a definite correlation with early and rapid development of shoot roots and is stimulated by the contact which a depressed habit causes between the first formed shoots and the ground. With reference to thickness of canes it is of interest to note that seedling canes, whether the result of self-fertilization or crossing, show transgressive inheritance in both directions. Reference has already been made to root development; in depth of penetration, capacity to penetrate stiff soils and resistance to water-logging, *S. spontaneum* shows a marked superiority which is largely inherited in its cross-bred offspring. In addition to these Indian observations Kutsunai (1926) has summarized the characters usually transmitted by Hawaiian canes.

In the absence of any clearly defined knowledge of the genetical constitution of the cane plant, the presence of mutations having their origin in the disturbance of the sexual processes are necessarily difficult to determine. That they arise can hardly be doubted since the parallel phenomenon of asexual mutation, or sporting, is well known. Indeed, some of the well-known varieties of cultivation as, for instance, the *White* and *Black Tanna*, which were isolated in Mauritius as sports of the *Striped Tanna*, have arisen in this manner. Similar sports, again in the colour of the cane, have been noted at Tucuman (1926). Indian experience is collated by Barber (1906) and a history of the earlier sports which have come into field cultivation is given by Deer (1921). There can be little doubt that mutations occur in other characters also, but the difficulties in the way of identifying such as are not optically determinable renders their identification a remote possibility. It is noteworthy that this tendency to sport is in some cases reciprocal.

The cane plant is not free from disease; in fact, the stimulus

which led to the work with seedlings arose from the susceptibility of the older canes to disease in varied forms. The appearance of *sereh* in Java in epidemic form and of root disease in Porto Rico and, to a lesser extent, in Barbados, raised in a severely practical form the question of securing resistant varieties. In Java the success achieved is largely due to a resistance introduced by the inclusion of *S. spontaneum* at some stage in the parentage. With the root disease the fungus *Marasmius sacchari* Wakker is intimately associated, but it is probable that the primary basis of the disease is physiological and the associated fungus only secondary. In these cases the source of varietal immunity lies most probably in a capacity to form, through a stronger root development or through some similar character, a robust plant capable of free development under relatively unfavourable conditions.

Mosaic is another disease which is responsible for extensive damage in many countries and of which the ravages have been met by the substitution of resistant varieties. Mosaic is now recognized as a virus disease, the infection of which is carried by *Aphis maidis* Fitch. Difficulty in countering the disease is complicated by the number of host plants, both wild and cultivated, which Brandes (1925) has shown to exist. Here again prevention is better than cure and the remedy is to be found in resistant varieties. The Indian canes generally exhibit a marked degree of resistance and, for this reason, *Uba* has become the predominant cane in South Africa. As in the case of *sereh*, it is the inclusion of these Indian forms, or of *S. spontaneum* itself, that is responsible for the immunity of many of the seedlings recently introduced. Stahl and Faris (1929) have studied the behaviour of a number of these forms in Cuba. The basis of this immunity is doubtful, but Venkatraman and Thomas (1928) have suggested that the presence of stiff unicellular bristles which are present both on the leaves of *Glagah* and *Kassoer*, may afford an explanation.

In Hawaii another disease of importance is that known as *eye-spot*, caused by *Helminthosporium sacchari* Berth. It, too, is being met by the raising of resistant varieties (Martin and Stender, 1926).

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CHAPTER XI

FRUITS

CITRUS AND ALLIED GENERA

THE species from which are derived those numerous forms of fruit which are classed under the general term, Citrus, are of Eastern origin. The original home of the group appears to be China and Cochin China, where its cultivation has been conducted from time immemorial and no truly wild forms are definitely known. As with other plants early introduced into cultivation, their classification offers considerable difficulty. Tanaka (1929–1930), in a series of papers, has discussed the question of the origin of the group and used his conclusions to supply a basis for classification. The more usual classification, based on the work of Swingle, is here adopted. Formerly classified under the single genus *Citrus*, the various forms are now usually placed in three genera, *Poncirus*, *Fortunella* and *Citrus*.

Poncirus. The single species, *P. trifoliata* Raf. occurs in northern China and the fruit is of no commercial importance. The species appears to contain several forms. It is commonly known as the trifoliate orange.

Fortunella. The genus was separated by Swingle (1915) who determined four species. It is native to south-east China, and the small fruits, known as kumquats, of three of the four species are made into preserves. The fourth species, *F. Hindsii* Swingle, is the Hongkong kumquat and has no commercial value.

Citrus. This genus contains all the more important commercial citrus fruits. It is native of south-east Asia, the Malay archipelago and the Pacific Islands. The various species have been carried round the globe and are now cultivated in all countries having a suitable climate. The more important forms are :—

C. medica Linn. The citron and source of candied peel.

C. Limonia Osbeck. The lemon.

C. aurantifolia Swingle. The lime.

C. maxima Merrill (*C. decumana* Murr). The Shaddock or Pummelo.

C. paradisi Macf. The pomelo or grape fruit.

C. Aurantium Linn. The sour, Bigarade or Seville, orange.

C. sinensis Osbeck. The sweet orange.

C. nobilis Lour. The king, mandarin or tangerine, orange.

C. mitis Blanco. The calamodin.

C. ichangensis Swingle.

The two latter are of small commercial importance, but the former of them has a potential value in breeding.

Of most of the cultivated species of *Citrus* numerous races exist which are distinguished for commercial purposes. Though the various forms, and especially the orange, are widely grown wherever the climatic conditions are favourable, the major problems are concerned with the recent development of large-scale production for export. The original source of the commercial supply of recent times was Spain and the Mediterranean region, but Florida, California and South Africa among other countries have developed a large export of the fruit. The West Indies still remain the main source of limes and their products, lime juice and citric acid. It is this organized production which gives rise to the numerous problems which centre on citrus cultivation, for such production demands grading and grade develops an importance almost equal to that of yield.

Citrus trees are readily propagated from seed or by the common methods of vegetative reproduction, budding, grafting and layering. Cuttings strike with difficulty, but a means of overcoming the difficulties attendant on raising cuttings has been described by Hunter (1931). The growth of seedling stock in the less highly specialized forms is commonly adopted, but in the more highly specialized forms which form the basis of organized production, budding is almost invariably adopted. The dual question of both scion and stock is, thus, raised.

In the flower of the *Citrus* the filaments of the numerous stamens

are united along their basal margins but are free above. The anthers rupture and the pollen is shed at the time of opening of the flower or even in the bud. The stigma lies at the same level as the anthers and becomes receptive when the petals have fully expanded so that the flower is slightly protandrous. The pollen is sticky and fertilization is effected by insects. Since the flower remains open several days, both self- and cross-fertilization are possible.

The complexity which attaches to the problem of fertilization in *Citrus* arises from the common occurrence of the phenomenon of polyembryony. Polyembryony, or the development of supernumerary embryos within the seed, the origin of which was shown by Strasburgher to be nucellar, results in the production of more than one embryo, and consequently seedlings, from a single seed. Since, in general, one only of these will result from nuclear fusion, the remainder will have an apogamic, or vegetative, origin and possess maternal characters only. This subject of polyembryony, in its bearing on *Citrus* problems, has been investigated by Frost (1926). He shows that different species and races of *Citrus* exhibit the phenomenon in very varying degrees and, in addition, that the number of embryos per seed varies considerably within the race. Thus, in the King mandarin, no polyembryonic seeds were found while, in the Willow-leaf mandarin, there occurred numbers varying from three to twelve with an average of 6·5. In many cases, therefore, it is impossible to determine whether a particular seedling has arisen normally as the result of fertilization or by nucellar proliferation. Should one seedling exhibit any divergence from the maternal parent, it may be assumed to have arisen in consequence of nuclear fusion; but the matter is not as simple as this, for Frost notes several instances of the occurrence of more than one divergent seedling from a single seed. In such cases, which concern the progeny of definite artificial crosses, the divergent offspring are "identical twins" and the question arises whether these arise by the fission of a single fertilized egg cell. Further, as will be more fully discussed below, since in *Citrus* vegetative, or bud, variation is commonly found, it is within the bounds of possibility that such asexual variation may occur

within the nucellar tissue which undergoes proliferation to form the apogamous embryos. That such is actually the case is the conclusion drawn by Frost from the study of certain albinistic and thick-leaved forms which occurred in his cultures. Further evidence has been collected by Toxopeus (1930) who, by using as pollen parent a race which would render the sexually derived seedling distinctive, obtained for Javanese species and races a percentage of apogamous embryos in some cases as high as 100.

In the presence of the above briefly noted complications of the phenomena usually accompanying fertilization, the difficulties in the way of determining the exact *rôle* of pollination and fertilization are considerable. The known facts concerning pollination have recently been set forth by Webber (1930) in a discussion of the influence, beneficial or the reverse, of associating a bee industry with citrus production. He concludes that *Citrus* is normally self-fertile, but agrees with Frost that the sex progeny resulting from selfing is weaker than that resulting from crossing. The work of Nagai and Tainiwawa (1926), however, has a bearing on this question. Though concerned with the question of the relative amounts of viable pollen produced by different races, they identified groups which are self-incompatible and other groups showing inter-group incompatibility. Webber showed, further, that pollination is unnecessary for the formation of fruit; but while, in the case of the Navel orange, the fruit was seedless, in the St. Michael orange it was seeded, the embryos presumably being apogamic in origin. This failure of certain varieties to produce viable pollen is well recognized, and this may lead to seedlessness, but the question whether the development of apogamous embryos requires the stimulation of pollination, remains unanswered. As a tentative conclusion, based on a comparison of the work of Osawa (1912) and Frost on the Navel orange which produces no viable pollen, it would appear that such stimulation is necessary; while the work of Nagai and Tainiwawa indicates that races differ in respect of the need for such stimulation. The further question, whether pollination followed by fertilization will always result in a viable sex embryo, also remains in doubt. The evidence indicates considerable competition

between the embryos within a seed and the existence of a negative correlation between the percentage of hybrids and total seedlings in crosses in which the seedlings of hybrid origin are readily distinguishable, seems to indicate that the competitive elimination of the sex embryo sometimes occurs. A study of nuclear behaviour adds still further to the complexity of the phenomena of fertilization. The original determination of chromosome number, N = 8, made by Strasburgher (1907) and Osawa (1912), has been corrected by Frost (1925) to N = 9. Longley (1925) has confirmed Frost's determination and extended it to a wider range of forms, but he found *F. Hindsii* to be a tetraploid form and therefore an exception. He notes, further, in the pollen mother cells frequent irregularities at diakinesis leading to greater or fewer numbers than the normal four pollen grains in the tetrad. He (Longley, 1926) has further shown that the chromosome number in the pollen mother cells of (*F. margarita* × *C. aurantifolia*) × *F. Hindsii* to be 13 bivalent plus 1 univalent and he suggests the possibility of securing a seedless form as the result of the unbalanced condition. Here, too, he finds irregularity in pollen formation, 17 per cent. of the tetrads having five, and 1·5 per cent. six, pollen grains. Similar irregularity in the development of the pollen mother cells, amounting to degeneration, has been shown by Uphof (1931) to occur in the Tahiti lime which is seedless, and Oppenheim and Frankel (1929), in an investigation of the reason why the Jaffa orange sets very little seed in Palestine, found, in addition to a low viability of pollen, degeneration of the embryo sacs. Interest centres, too, on the thick-leaved form, the appearance of which has been frequently noted by Frost in certain varieties of orange, grape fruit, tangerines and in one variety of lemon, sometimes to the extent of several per cent. From his determination of the chromosome number in this form derived from the orange (Frost, 1925b) this form would appear to be a tetraploid, and the evidence would appear to suggest that the same holds good for the form in the other species in which it is found, but frequent irregularities occur in chromosomal behaviour in the pollen mother cells. He further suggests that this form is apogamic in origin.

The practical bearing of this chromosomal constitution of *Citrus* is dual. In view of the common commercial practice of raising stock through budding, it bears, on the one hand, on the question of suitability of stock, on the other, on the choice of scion. Where polyembryony is well developed the mass of the seedlings will be apogamic in origin and, having the maternal constitution only, uniform. Whether such uniformity will occur in the intermingled seedlings of sexual origin will depend on parental purity. The whole of the evidence assembled by Frost (1926) is strongly suggestive of a complex heterozygous constitution. He has shown that sexually produced offspring are decidedly more numerous with crossing than with selfing, while the offspring forming the F_1 of a cross often vary greatly in vigour as well as in form, a variation which led Swingle (1913) to propound his theory of zygotaxis. The facts, however, appear to be explainable on the basis of heterozygosis combined with the occurrence of a number of lethal, or semi-lethal, factors, the occurrence of which in homozygous condition resulting from selfing leads to abortion of, or lack of vigour in, the sexual embryo. Thus, purity of stock, that important factor in commercial production where the normal stock used for budding is of seedling origin, largely depends on the use of seedlings of apogamic origin.

The subject has been studied from a practical aspect by Webber (1930b), who concludes, from a comparison of the area of cross-sections of trunks, that large seedlings produce large budded plants and that subsequent selection of the budded trees is unnecessary if a rigid selection of nursery stock be made. Toxopeus, as the result of his work to which reference has already been made, proposes, for the purpose of raising seedlings for stock, the sowing of seed derived from flowers artificially fertilized by pollen of a species sufficiently divergent to ensure the recognition of the sexually produced seedlings which can then be eliminated. Attention is drawn to the same fact by Eyre (1931) who suggests the adoption of layering as a method of securing uniformity of stock.

A further phenomenon common in *Citrus* and of considerable practical importance, raising as it does the question of chromosome

constitution in relation to the scion, is the frequent occurrence of bud variation. Some of these somatic variations are striking, others are less obvious and may even concern only the yield capacity of the plant. The importance of a careful selection of bud wood, thus, becomes a matter of considerable interest, and it should be taken only from trees showing no limb variation. Shamel and his colleagues (1918–1925) have made a very detailed study of the phenomenon in its practical bearing, and conclude that the mixture commonly found in the orchards of Navel and other oranges is due to faulty selection of bud wood. Their results show what is possible by careful selection. What little is known as to the cause and cytological basis of such variation is discussed by Frost (1926). The frequency of somatic variation in *Citrus* suggests the possibility of its occurrence in the nucellar tissues undergoing proliferation to form apogamous embryos, and a further source of complexity is, thus, added to the raising of nursery stock.

Disease in many forms is prevalent in *Citrus* orchards, but the extent to which these develop is largely a question of cultural conditions. Choice of stock is also of considerable importance, for there are notable differences in the degree of resistance. Gummosis, a disease of which the causative organism is *Phytophthora citrophthora* Sm. and Sm., has been studied by Klotz and Fawcett (1930), who tested seventy-eight species and varieties for resistance. In these tests the sour orange proved very resistant, while the lemons were most susceptible. Klotz (1927) has shown that the resistance is due to some cellular product of the host which has an inhibiting action on the fungoid enzymes. Toxopeus (1931) has drawn attention to the influence of immunity of scion on the stock.

Withertip, caused by *Glœosporium limetticolum* Clausen, which first appeared in Trinidad in 1917 and has since spread throughout the Antilles, has seriously threatened the Lime industry of those islands. The question of the relative susceptibility of *Citrus* varieties to the disease has been studied by Fulton (1925), who finds susceptibility to be confined to the West Indian, and the Dominican thornless, lime. His results indicate that susceptibility

is not dominant. Efforts are being made in Trinidad to find a resistant variety of lime having a suitable acid content as also to raise resistant races by crossing. These efforts are described by Williams (1929).

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THE BANANA (*MUSA spp.*)

The genus *Musa* contains a number of economic species of which those providing the fruit known as the banana are the best known and the more important, forming as they do, with the plantain, a vast food supply for numerous tropical races as well as an important subsidiary supply to many temperate countries. Certain species, too, notably *M. textilis*, are grown for their fibre.

The members of the genus Musa, of the natural order *Musaceæ*, are characterized by a short subterranean rhizome from which arises a pseudostem, formed by the closely apposed leaf-bases and attaining in some species a height of 20 feet. The inflorescence arises from below and forces its way to appear from the apex of the pseudostem. When the bunch ripens the stem dies and growth is carried on by lateral suckers. This inflorescence is a dense raceme, or spike; the flowers arise in clusters, each of which is subtended by a large bract. The female flowers lie at the proximal, and the male at the distal, end of the inflorescence, the two types of flowers being separated by a greater or less number of neutral flowers. The clusters of female flowers are limited in number and develop into the "hands" of commerce; the clusters of male flowers are indefinite in number, since the spike continues to grow till the death of the stem. The male flowers on a single spike may, thus, number over 1,500.

Of old-world origin, the plant is now cultivated throughout the tropics wherever adequate moisture occurs, for they are moisture-loving plants. The classification of the genus offers considerable difficulty, since the plant does not lend itself to study except in the field, and varietal determination is still more difficult owing to the adoption of local names in the many countries of cultivation. Decisive information on these matters will only result from the establishment of a collection of living material such as is now in process of accumulation at the Imperial College of Tropical Agriculture in Trinidad, and through which Cheesman (1932)

has been enabled to determine the identity of the Gros Michel with the Malayan Pisang Embun. Baker (1893) has given a synopsis of the natural order; Fawcett (1913) has given a descriptive list of sixty-nine species of the genus *Musa*, while Howes (1928) has described the forms found in the east. The more important economic forms have been generally, but provisionally, classified as follows :—

M. textilis Née. A tall plant grown in the Philippines for its fibre which forms the Manilla hemp of commerce.

M. sapientum L. The main banana of commerce of which an indefinite, but large, number of varieties exists. The most important of these is the *Gros Michel* of the West Indies and Central America.

M. paradisiaca L. More usually considered a variety of *M. sapientum.* It provides the plantain.

M. Cavendishii Lamb. A dwarf plant 4 to 6 feet high. Introduced from southern China *viâ* Mauritius to the Canary Islands and to a lesser extent elsewhere, it has become known as the Canary banana.

Breeding in the group is limited to the banana and has only recently been undertaken as the result of economic pressure. The vast trade in this fruit from the tropical islands of the West Indies, particularly Jamaica, and the mainland bounding the Gulf of Mexico is based on the single variety the *Gros Michel.* Thence special boats, fitted for the longer journeys with cool storage, carry the fruit in bunch to America, Canada and Europe. Thus there is raised, in addition to the usual desiderata of yield and quality of product, the question of capacity to meet the conditions of transport. The requirements are partly physiological (Wardlaw and McGuire, 1931); partly they are morphological, a tough skin and recurved fingers (fruits) which are best adapted for transport in the bunch without packing. It is the suitability of the *Gros Michel* in these respects that is largely responsible for the wide extension of the cultivation of this variety. Further, the presence of seed as a common phenomenon in the fruit constitutes a serious blemish. The breeding problem consequently offers certain unique features inasmuch as, starting with a seedless

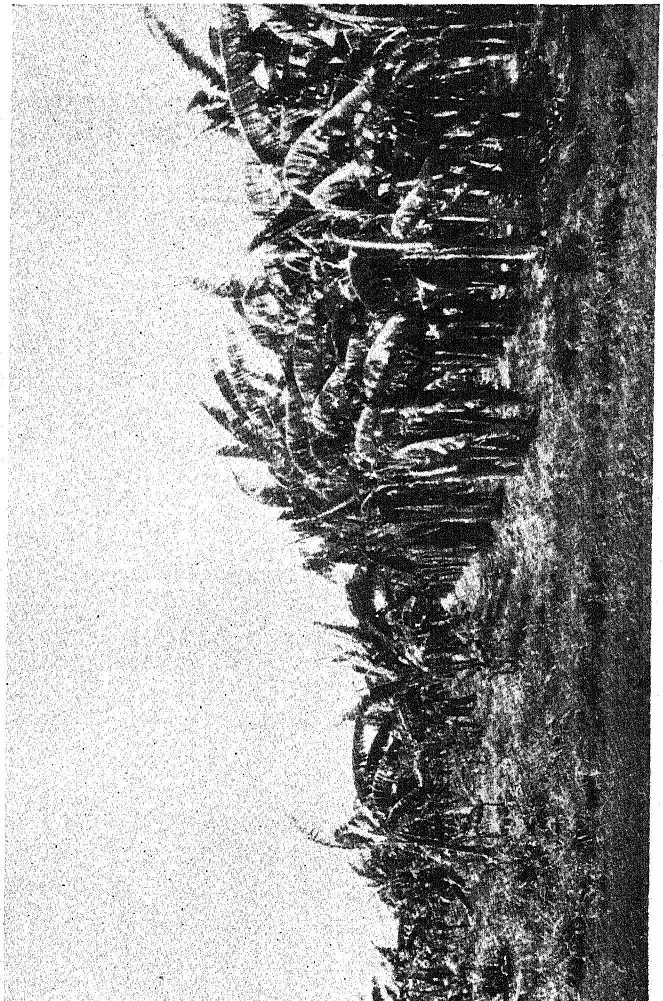
plant, a seeded stage must be passed through to provide material for a recombination of characters and a seedless form recovered. The weakness of the *Gros Michel* lies in its susceptibility to the Panama disease. This disease, caused by the fungus *Fusarium cubense* E. F. Smith, has spread throughout the West Indian and American banana fields, with the exception of Colombia, since it was first noticed in Porto Rico in 1903 ; and large areas have been put out of cultivation through its ravages. The main problem is, thus, to procure a banana having the desirable qualities of the *Gros Michel* with the added character of resistance to Panama disease. Co-ordinated attempts to breed the banana have only recently been undertaken at the Imperial College of Tropical Agriculture, and Cheesman (1931) has given so detailed a summary of these, together with a review of other work, that it is only possible here to summarize his account.

Within the range of species of *Musa* all stages are found from forms, such as those which supply the bananas of commerce, with little or no viable pollen and developing fruit without fertilization, to forms, such as *M. malaccensis* Ridl., with abundant pollen and free formation of viable seed. This progressive sterility may take various forms. In the extreme case the reproductive organs of both sexes are abortive up to 99 per cent., and failure to set seed is complete. Phenocarpic seed may, however, be formed and seed which, though apparently perfect, fails to germinate. In other cases germination may result in a seedling weakened, apparently, by certain semi-lethal characters. An initial difficulty, therefore, is at once met with in obtaining a sufficient number of seedling plants to provide material for selection. For this purpose *M. malaccensis* Ridl. and *M. ornata* Roxb., have been used as pollen parents, but even here the percentage of viable seed is very low. Thus, with the *Gros Michel*, from 71 bunches pollinated 39 seeds only were obtained, and of these only 3 germinated, while from 61 bunches of the *Fillbasket* variety 196 seeds were obtained of which only 14 germinated. There appears to be evidence of at least partial self-sterility, so that a variety in pure culture offers little prospect of developing seed-bearing fruit, a point of economic significance,

and attempts to increase the seed supply are in progress by the interplanting the two varieties in the proportion of five fruiting, to one pollen-producing plant and trusting to fertilization by natural agency. Only the earliest seedlings have progressed to the fruiting stage, and of these, I.C. 1, a cross between *Gros Michel* and *M. malaccensis*, proved resistant to Panama disease. When selfed, only 1 seedling was obtained from 12 seeds, the product of 57 bunches; back-crossed to *Gros Michel*, 24 bunches yielded 1 seed which failed to germinate; back-crossed to *M. malaccensis*, seed set freely, but the seedlings proved economically useless.

These results were secured from the earlier experiments based on the usual procedure of attempting to incorporate into the *Gros Michel* favourable characters, especially resistance to disease, derived from other species. From recent work, however, it appears that the sterility typical of the edible bananas is correlated with chromosomal constitution. The earliest investigations in this connection are those of Tischler (1910). In 1914 d'Angremond (1914) determined the number of chromosomes in *M. basjoo* and *M. ornata* as 22 diploid and that of the *Gros Michel* provisionally as 32. In a further paper d'Angremond (1926) has recorded his investigations on the nuclear constitution of *M. ornata* and *M. zebrina*. Both possess 22 chromosomes as does the F_1 between the two and, on back-crossing this with *M. zebrina*, a range of numbers between 22 and 33 is obtained. White (1928), in a very detailed study of the whole field, suggests that the basic chromosomal number of the genus *Musa* is 8 diploid, and he tabulates a polyploid series up to $12n$ (48) chromosomes. By apogamy in one or both parents the higher members of the series are obtained, and it will be noted that the same number may be obtained in more than one way, in one case the chromosomes being balanced, in which case the plant will be fertile, and in the other, unbalanced, in which case the plant will be sterile. The *Gros Michel* and most of the edible bananas fall into this latter group, and he suggests a hybrid origin for the *Gros Michel* between parents having 40 and 24 chromosomes respectively. On this hypothesis the chance of securing a favourable plant to replace the *Gros Michel* will be,

PLATE VIII



Musa sapientum L. *Right:* I.C.1, healthy; *Left:* Gros Michel, practically destroyed by Panama disease.

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not by employing that plant itself, but by the search for races possessing 40 and 24 chromosomes respectively and crossing the two. Of the latter numerous races are known, but White records of the former only two.

The conclusions of White require confirmation. As has been noted, d'Angremond found *M. zebrina* and *M. ornata* to possess 22 chromosomes. Cheesman has further found *M. malaccensis,* the parent used to cross with the *Gros Michel*, to possess 22 chromosomes. I.C. 1, the F_1 of this cross, he found to possess 43 ($16 + 16 + 11$) chromosomes and its pollen 21. He inclines to the view that the desired plant will be obtained by crossing the F_1 of the *Gros Michel* with 43 chromosomes with a seeded resistant race having 22 chromosomes ($21 + 11 = 32$). Further investigation alone can provide the solution, but there can be little doubt that detailed cytological investigation will play an integral part.

Since the above was written, Cheesman, in a personal communication, has kindly supplied an account of his later work which throws a new light on the chromosome numbers of the *Musa* group. He finds the wild forms, *M. zebrina* and *M. malaccensis,* as before, to possess 22 chromosomes, but that the *Gros Michel* possesses 33, not 32, and the cross *M. malaccensis* × *Gros Michel* 44, not 43, while the F_1 of this cross back-crossed to *M. malaccensis* possesses 33. It would appear, therefore, that the basic number of chromosomes in *Musa* is 11, that *M. malaccensis* is a diploid and the *Gros Michel* a triploid. This interpretation supports the view that the commonly accepted classification of the genus is provisional and likely to undergo revision in the light of further work on the chromosomal constitution of the various forms. It also has a direct bearing on the problem of raising a seedless form.

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CHAPTER XII

TOBACCO (*NICOTIANA spp.*)

TOBACCO, in all its forms, is the product of the leaf of two of the forty odd species of *Nicotiana*, a genus belonging to the natural order *Solanaceæ*. They are *Nicotiana Tabacum* L. and *Nicotiana rustica* L., and of these the former is the chief source. These two species of economic importance are of tropical American origin, but their cultivation has spread round the world and well into the temperate zones. Tobacco was introduced into Europe through Portugal in 1539, and its introduction into India, in which country *N. rustica* is widely grown, appears to have been the work of the Portuguese missionaries early in the sixteenth century. Though it had previously been cultivated by the Spaniards in San Domingo, its first systematic cultivation was undertaken in Virginia about 1612.

With the passage of time the use of tobacco has undergone many modifications, and the methods by which it is smoked at the present day are numerous. For each of these forms definite characteristics are required. The qualities required in pipe tobacco differ from those required in cigarettes, while the cigar wrapper requires still other qualities differing, again, from cigar filling tobacco. Further, to obtain the standard forms, of which there are many both of pipe and cigarette tobacco, not only are different standards of the crude tobacco required, but these are submitted to a process of blending. If, too, the demand for tobacco in the form of snuff is diminishing owing to the passing of the snuff habit, a new demand is arising for tobaccos high in nicotine content for the manufacture of insecticides. Of a totally different order is the tobacco, made up with *gur* (crude sugar) and spices into cakes, used so largely in India for smoking in the *chilam*. The development of the tobacco industry is, in consequence, marked by a progressive specialization to meet the requirements

of the various markets. It is a specialization which is carried back to the varietal differentiation of the plant.

The matter is not, however, as simple as this statement implies. Many of the factors on which quality of the product depends are found to be influenced by environmental conditions. The most striking instance, perhaps, is that of cigar wrapper tobacco, for which a thin lamina and fine venation is requisite, qualities which are produced by growing the crop under artificial shade given by cloth. But even here special varieties must be grown if the requisite quality is to be secured. Other differences are traceable to soil, and, in fact, the response of the plant to varying soil conditions is so definite that market quality may be entirely changed by transfer to a new locality. The response is even greater than here indicated, for it is quite possible materially to affect the quality of the crop by manurial treatment. Excess or deficiency of potassium and chlorine particularly produce symptoms which may be detected in the product. In South Africa, where kraal manure is largely used for air-cured tobacco, the dressing will be doubled if a dark heavy leaf is desired in place of bright leaf (Taylor, 1924). Coolhaas (1930) has noted the effect of manures, especially sulphate of ammonia and superphosphate, in improving odour and flavour. Specialization is, therefore, extended to include cultural methods.

Quality is dependent on yet another set of factors. The alkaloidal constituents to which tobacco largely owes its peculiar properties, do not exist in the living plant as such. They are the products of certain processes to which the leaf is subjected after the plant is cut. The cut plants or leaves, according to the process adopted, are first dried and then cured. Drying is a preparatory process requiring delicacy of manipulation if the correct colour is to be obtained, while curing is a fermentative process and, like all such processes, demands a high degree of skill if the final product is to conform to the required standard.

In these circumstances it is a matter of more than common difficulty to determine to what extent characters which are desirable, are dependent on factors inherent in the plant itself and, therefore, material for the exercise of the breeder's art.

Certain characters obviously find their basis in the plant itself. Of such a nature are characters which affect yield, such as number, and size, of leaf; factors adapting the plant to locality such as period of growth and certain of the factors affecting utility such as shape of leaf, of especial importance in the case of wrapper tobacco, since, on shape, largely depends the amount of waste in cutting the leaf into the required strips, or as venation, that is, the angle which the secondary veins make with the midrib. Other characters, especially those which affect quality, are less obviously but, in many cases, no less certainly to be traced to the plant, and there is, in fact, a distinction between the races of tobacco used for the main forms of smoking sufficiently great to justify a varietal definition. One pertinent fact, however, arises out of this high specialization; local conditions play so important a part in the moulding of the ultimate product that the best results will follow only from breeding in each defined tract for the particular conditions there prevalent.

The most extensive study of the tobaccos is that of Comes (1899, 1905). The genus is, according to general acceptation, divided into three or, by some, into four, sections, two of which, *Tabacum* and *rustica*, as the names sufficiently indicate, are represented by the two economic species. The numerous forms of *N. Tabacum* L., the economic representative of the first group, are arranged by Comes into six groups on a basis of colour and size of flower, shape and texture of leaf, height and number of leaves. These groups are:—

Var. *fruticosa*, a native of Mexico and Brazil.

Var. *lancifolia*, in which he places the well-known *Burley* tobacco.

Var. *virginica*, in which are included such tobaccos as *Virginia bright*, *Orinoco*, *Kentucky yellow* and so on.

Var. *braziliensis*, in which are included *Brazil*, *Bahia*, *Maryland* and others.

Var. *havanensis*, in which are the cigar wrapper tobaccos of Sumatra, Java and America.

Var. *macrophylla*, a large-leaved tobacco grown in Cuba, Turkey, Egypt, India and elsewhere.

The Howards (1910) have attempted a classification of the Indian forms and recognize fifty-one types. Their classification is based on leaf form and length of internode. As they point out, however, after attempting to fit the Indian types into Comes' classification, since the varieties are completely interfertile, types are to be found cutting across the varietal differences named by him. It would appear, therefore, that any classification within the species can be little more than a convenient key having a certain practical utility but lacking any phylogenetic significance such as a systematic varietal classification implies.

N. rustica L., of secondary importance in the economic aspect, is not so polymorphic a species as *N. Tabacum*. It, too, is divided by Comes into six varieties.

Var. *texana*, the variety supposed to have been the first introduced into Portugal.

Var. *jamaicensis*, wild types of central America and the West Indies.

Var. *scabra*, a form hardly used commercially.

Var. *brazilia*, cultivated in Brazil and Europe for snuff.

Var. *asiatica*, supplies the so-called Syrian tobacco and largely used for snuff.

Var. *humilis*, a small form used for snuff.

The races cultivated in India, where it is extensively grown owing to its short season which enables it to be planted on the retreating flood in Bengal and also permits the seed to be sown after danger of damping off during the rains have passed, have been studied by the Howards (1910) who base their classification on internode length and form of inflorescence. Here, again, the remarks which apply to the classification of *N. Tabacum*, have equal force. The Howards were unable to fit the Indian types into Comes' scheme of classification.

The varietal classification of these two species is closely bound up with the major classification of the genus, itself by no means a simple matter. In recent years efforts have been made to determine the phylogenetic relations of the various species on a basis of compatibility and chromosomal constitution. Much study has been devoted to the determination of chromosome numbers,

and these have been found to range from N = 8 to N = 24 with intermediate values of 10, 12 and 16. Further, all stages of compatibility are found in inter-specific crosses from the formation of fully fertile hybrids to complete sterility, and these different degrees of compatibility cut across the divisions marked by chromosome number. Any consideration of this body of investigation lies outside the scope of the present subject and has, moreover, recently been reviewed by East (1928). It is here sufficient to say that the two economic species, *N. Tabacum* and *N. rustica*, both carry the maximum number of chromosomes found in the genus (24) and that compatibility between the two species is very slight. Christoff (1928) failed to obtain seed from the cross *N. Tabacum* × *N. rustica*, while, from the cross *N. rustica* × *N. Tabacum*, he obtained less than 1 per cent. germination, and the two hybrids raised were only slightly fertile; in habit of growth they were intermediate, with the leaf petiolate. Rybin (1927) working with this cross, succeeded in raising two plants. These plants produced sterile pollen, but gave rise to a further generation when their flowers were pollinated with pollen of *N. Tabacum*, *N. rustica* and other species of *Nicotiana*, though seed was formed with difficulty and few in number. He carried out a detailed study of the nuclear structure and behaviour which showed one of these plants to be a triploid having 72, and the other a tetraploid having 96 chromosomes. The subject has also been investigated by Savelli (1927) and Eghis (1927b).

A further point which has complicated the study of the genus and, particularly, that of the species *N. Tabacum*, has been the discovery, originally established by Haig Thomas (1909, 1913) of the occurrence of apogamy in the genus in a Cuban variety of *N. Tabacum*. The extent to which parthenogenesis occurs is still open to argument, as are the environmental conditions which stimulate it, if such there be. East failed to find apogamy either in *N. Tabacum* or in some sixteen other species (Wellington, 1913) nor was Wellington (1913) able to induce it by artificial means, though East obtained in certain crosses maternal plants sometimes with, and sometimes without, an admixture of true hybrids. As the existence of parthenogenesis to the extent indicated must

introduce material errors in breeding tobaccos in which it occurs, the subject was submitted to detailed study in the Indian forms by Mrs. Howard (1913). She tested fifty-one Indian types of *N. Tabacum* and obtained, in all, five seed-bearing capsules in 10,000, a percentage so small as to bear the interpretation that they were errors in technique. Further, in all her crosses, she failed to detect a single individual resembling the mother parent. Later Howard and Kashi Ram (1924) repeated the work in India, using the varieties studied by Haig Thomas. They found parthenocarpy to occur in the Cuban variety and in crosses between the two varieties studied, but no evidence of parthenogenesis. Mrs. Howard (1924), working with *N. rustica*, obtained no evidence of parthenogenesis or parthenocarpy. Savelli (1929) has also studied the question in certain other forms of *N. Tabacum*, while, later still, Tollenaar and Middelburgh (1930) studied a number of varieties and obtained no evidence of parthenogenesis, though, in some of the varieties, a strong tendency to parthenocarpy and phenospermy was observed.

Tobacco affords an example of that feature so common in cultivated plants of which there is a trade in seed, an intense confusion in varietal terminology. This confusion is, perhaps, greater in the case of tobacco than in any other crop owing to the variation in form induced by climatic and other environmental conditions under which it is grown. For a long time the plant, especially *N. Tabacum*, has been selected on an empirical basis and the view was persistently held that change of environment induces variation. This is a view which, in the generality of cases, rests on no solid foundation, though Krapivine (1928) has recently claimed to have raised by a reduction of plant food forms of *N. rustica* having heritable differences in time of ripening and in number of leaves. The differences which separate one variety from another are very subtle and may be readily overlooked until a change of environment adds emphasis to them. Further, as detailed study has shown, opportunities for cross-fertilization are sufficient to break down uniformity unless precautions are taken to ensure self-fertilization. The numerous forms now grown have, in practically all instances, arisen as the result of empirical

selection; the trained eye, whether of the seedsman or tobacco grower who raises his own seed, observes a particular plant as approaching more nearly to his ideal than the mass of his crop and he preserves it as a seed parent. These differences may be marked or they may be subtle. An example of the former is given by the history of *White Burley*, which was derived from a few strikingly light-coloured plants isolated by Webb in a field of *Red Burley*. The history of *Uncle Sam* tobacco, isolated by Shamel early in the century, illustrates selection from the marked variability resulting from change of locality. Similar, too, is the history of tobacco in all countries into which it has been introduced, while in India, direct isolation of plants in the crop as commonly grown has resulted in great improvement of the product. What is the true nature of these variations, whether separation out of homozygous forms from a heterozygous community, or mutations, as is probably the case in some instances, must remain a matter of speculation since those responsible for the selection have been concerned in most cases only with the practical issue. Occasionally more is known about the origin of a commercial form, and Johnson (1919) has placed on record the history of the *Connecticut Havanna No.* 38 improved strain which illustrates in greater detail than is usually available the methods of selection. From thirty-five plants raised from presumably pure-bred seed of *Connecticut Havanna*, line cultures were raised which indicated the presence of three fairly distinct types, but which gave remarkable uniformity within each line. Two of these types were definitely distinct from each other as well as from the main type and both possessed characters offering a commercial advantage over the main type. In 1910 these two strains were crossed and an F_1 obtained which showed to a very large extent a very desirable intermediate condition, a condition approximating to the ideal in mind. In subsequent generations no identifiable segregation was observed and it appears from this, and other, observations of the author that, under certain conditions where closely related strains are crossed, blended inheritance occurs. The new strain was grown for four years before being distributed and, by 1919, ten years after isolation of the two strains, the estimated area under the new

strain had reached 10,000 acres. This tendency towards blended inheritance has been studied by Schweizer (1928).

More rarely is the production of a variety the result of direct synthesis, the formulation of the ideal plant and the deliberate combination in one plant of the desired characters. Such an attempt, ending in the successful attainment of the object, has been described by East and Jones (1921) who developed the *Round Tip* tobacco from a cross between *Broad Leaf* and *Sumatra.*

The inflorescence of the tobacco plant is a much-branched cyme, the lateral axes of which develop in descending order, the flowering period lasting some thirty days. The flower is typically pentamerous, but, as in so many cultivated plants, considerable irregularities occur even on the same plant. The buds usually open in the morning or early afternoon. There occur considerable differences in the details of fertilization in different varieties. The Howards and Abdur Rahman (1910) have studied these differences in the Indian forms of both economic species. In *N. rustica* the anthers burst in the bud before the corolla opens, and at this time the stigma is receptive so that homogamy is the rule. The relative position of the stigma and anthers, however, varies considerably at the time the flower opens, the anthers being below, opposite, or above, the stigma. The stamens themselves are not of uniform length. They recognize three classes :—

(1) Stamens much longer than the style. The four longer stamens bend over so that the stigma is invisible.

(2) Stamens about the same length as the style. This intermediate condition is the commonest. Slight differences in length will influence the possibility of cross-fertilization.

(3) Style much longer than the stamens. This is an uncommon condition which they found in only one instance. In this type self-fertilization had to be effected artificially.

In *N. Tabacum* they found that normally the anthers burst as the petals unfold. Here again they found a range of relative positions similar to that found in *N. rustica.*

From these, as well as from many other investigations by different observers, there is no doubt that cross-fertilization can take place in the field though the extent will differ in different

varieties. Tollenaar and Middelburgh (1930) investigated the question in a somewhat different manner. They pollinated emasculated flowers with their own pollen and subsequently with pollen of a different variety at varying intervals. The offspring showed hybrids varying in number with the time interval from 27 per cent. at two and a half hours to 10 per cent. at eight hours. There is, thus, a considerable time interval during which foreign pollen, carried by insects, will be effective in spite of the earlier application of the plant's own pollen. The crop is a seasonal one and the maximum variation between the time of flowering of different types is small relative to the length of time during which pollen will remain viable.

The genetic analysis of the tobacco plant, of whichever species, is a matter of considerable difficulty owing to the large amount of variability of a quantitative nature which it exhibits. There is no reason for suspecting, however, that the methods of inheritance differ in any essential particular from those exhibited by other plants. Allard has studied in *N. Tabacum* the flower colour (1919a) and gigantism (1919b) and, in *N. rustica*, a light-stemmed *aurea* form (1919c). In the first case he found carmine dominant to pink, and white recessive to both, but the inheritance was not simple, since forms occurred in which a trace of pink, hardly distinguishable from white, appeared. Further studies of flower colour have been carried out by Clausen and Goodspeed (1921), who give a trifactorial interpretation, while an interpretation of a somewhat different nature, though involving three factors, is given by Christoff (1925).

Gigantism, or indeterminate growth as it is alternatively called, in which the stem is prolonged vegetatively, Allard found to be recessive to normal growth. But here, again, the matter is not so simple. Gigantism has been observed in many types and in many countries since it was first recorded by Hunger (1905) in the *Deli* tobacco of Java, and it has not been shown that this character is due to the same factor in each case. The plants exhibiting the character appear to arise as mutations, and Lodewijks (1911a) found intermediate forms which gave approximately 25 per cent. giants together with intermediate and normal.

The strains of tobacco showing gigantism have a further interest in that it was from observations on them that Garner and Allard (1920) drew their conclusions on the photoperiodic control of reproduction. They found that indeterminate plants produce flowers when the length of day was artificially shortened.

The *aurea* form of *N. rustica* investigated by Allard proved to be a simple recessive to normal. In *N. Tabacum* the inheritance of the *aurea* form, which was studied by Lodewijks (1911a) was apparently not so simple, for he obtained ratios departing widely from the normal 3 : 1 and, moreover, in reciprocal crosses the ratios were markedly different. These results may be compared with those of Kajanus (1924) in a cross between a dark-leaved *Maryland* tobacco and the light-leaved *White Burley*, in which the light-leaved form was recessive with a ratio approximating to 15 : 1 suggestive of a bifactorial difference.

Few other characters have been shown to be capable of interpretation on a simple factorial basis. A fasciated form of *N. Tabacum* which arose in a Cuban variety, was studied by White (1916). Here a single factor was concerned, with the heterozygous condition intermediate. In *N. rustica* Howard (1924) found the undulate leaf margin to be due to a single factor, but not dominant to the flat leaf margin ; while East (1928) noted brown seed as being dominant to white seed.

When attention is turned to other characters, especially to those which have an economic value, a more complicated condition of affairs is disclosed. Much labour has been spent in the analysis of such characters and many, and very detailed, observations have been placed on record, notably those of Hayes, East and Beinhart in Connecticut ; Setchell, Goodspeed and Clausen (1921) and their associates in many publications of the University of California ; Howard (1913) and Howard and Kashi Ram (1924) in India and in the Netherland East Indies by numerous workers whose results have been reviewed by Tollenaar and Middelburgh (1930).

Time of flowering, apart from the extreme form known as gigantism to which reference has already been made, was investigated by Howard (1913) in the case of certain of the Indian types

Type I

F_1 (Type I × Type XVIII)

Type XVIII

Nicotiana rustica L. Howard's Types.

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[*To face p.* 226.

of *N. Tabacum*. In all cases the F_1 was intermediate, but in the F_2 transgression was found to occur in both directions, and she succeeded in isolating strains some of which were slightly earlier than the early parent, while others were much later. The series in all cases proved too complicated to attempt factorial analysis. The number of leaves borne by a plant of *N. Tabacum* was also subjected to detailed analysis by her. This is a character which, though to some extent dependent on environment, appears to be independent of height. The results are interpretable on the assumption of a basic condition with 19 leaves, combined with an indefinite number of independent factors which can add to this number up to a total of 35, the maximum found in the Indian types. East (1928) records that, working in conjunction with Hayes on a cross between *Havanna* and *Sumatra* tobacco, he was able to isolate strains with any desired number of leaves from 12 to 30. The lowest coefficient of variability obtained for any strain was 4·0, which he considers a measure of the residuum of fluctuating variability in a genetically homozygous strain. This is variability of the nature of that investigated by Jensen (1916). More recently Davidowicz (1928) has attempted a mathematical interpretation of leaf number in the course of which work he studied many other characters and attempted to trace correlations between them. The only correlation he found was between leaf number and earliness.

Equally detailed were Mrs. Howard's investigations on height both in *N. Tabacum* (1913) and *N. rustica* (1924). Height is due less to number of internodes, which would affect the number of leaves, than to length of internode, and actually some of the shorter types carried the largest number of leaves. In both cases height in the F_1 was not strictly intermediate between that of the two parents, and in this respect differed from the other quantitative characters observed. Though different results were obtained with different crosses, height usually approximated to, and in some cases exceeded that of, the taller parent. The occurrence of transgression in the F_2 is well shown by the cross Type 23 × Type 38, the respective mean heights of which were 133 and 130 cm. with the F_1 132 cm. In the F_2 and subsequent generations heights

ranging from 65 cm. to 205 cm. were obtained. In another case a strain with an average height of 50·8 cm. with limits of variation 35 cm. to 65 cm. was obtained from a cross, the shorter parent of which had an average height of 87 cm. In this case the limits of variation of the new strain and of the shorter parent do not even overlap. These results indicate a complexity too intricate for detailed factorial analysis. In *N. rustica* a similar condition appears to hold, but the distinction between short and tall types is more definite and appears to be due to a single factor; but other factors probably modify the height within these major divisions. A further complication arises from the fact that many of these factors appear to be connected with the type of inflorescence. As far as her analysis goes, it appears to indicate two major factors, that converting a short plant of any kind into a tall plant with open inflorescence, and another, affecting the inflorescence only, converting a compact form into an open one. Such a genetical constitution explains the major observation that, in the presence of the factor for tallness, either in the homozygous or heterozygous condition, a compact inflorescence does not exist. With these results of Mrs. Howard may be compared those of Honing (1927), who found a dwarf race having an average of seven leaves only. In this case the results showed a monofactorial difference between dwarf and normal with the dwarf condition dominant.

In considering that important character, leaf shape, Mrs. Howard found the characters, ratio length to breadth, position of greatest width, amount of indentation at the apex, amount of indentation at the base and shape at point of insertion (auriculate or not) were all inherited independently. Lodewijks (1911b) studied in great detail the length and breadth of leaves in different types as well as the correlation between these two measurements within the types. His conclusions agree with the general conclusion of the Dutch workers that the two characters are inherited independently. They are, however, characters which are liable to extensive modification through environmental influences and the effect of these influences is largely eliminated in the measurement of the ratio between them as selected by Mrs. Howard.

PLATE XI

Nicotiana Tabacum L. F_1 of F_1 (Type I $\times$ Type XVIII) $\times$ Type XVIII.

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[*To face p.* 228.

Of all these characters the least complex is the leaf base, for, by crossing two races in which the leaf bases differ, a petiolate form was obtained which at once bred true. She considers the petiolate form to be a sessile leaf with deep indentations. The leaf base has been further studied by Setchell, Goodspeed and Clausen (1922) who suggest a trifactorial interpretation; while further studies of the leaf base have been made by Kellaney (1925) and Bourzev (1928), who deduces an even greater factorial complexity. The inheritance of the remaining characters she found to be extremely complex. She also made somewhat less detailed observations on the undulations of the leaf and frilling of the leaf margin. The latter of these proved, as already noted in the case of *N. rustica*, to be due to a single factor. Finally she attempted a partial analysis of that character of the flower which concerns the relative position of the anthers and stigma. Her observations indicated a mono-factorial difference between the two conditions anthers above, and anthers surrounding, the stigma; and a bi-factorial difference in the case of anthers above and anthers below the stigma. It may be observed, however, that this interpretation appears very simple when it is remembered that two independent measurements are here involved, the length of the filaments and the length of the style.

Quality is a still more elusive character, to speak more accurately, complex of characters and, as already noted, is subject to wide modification under different environmental conditions. It covers not only such characters as odour and flavour, which have a direct appeal to the consumer, but others, such as burning, or fire holding capacity which has been studied by Coolhaas (1930). Little progress has been made in the analysis of these characters.

As has been noted, the increasing use of insecticides has created a demand for high nicotine content in tobacco, and for this *N. rustica* is usually employed as having a generally higher nicotine content. Over twenty years ago Garner (1909) showed the possibility of breeding strains with high and low nicotine content and the subject has been further examined by Sengsbusch (1931), who indicates the possibility of isolating strains having different

capacities for developing nicotine and even nicotine free (under 0·08 per cent.). He also indicates the apparent independence of aroma and nicotine content. Kostoff and Popoff (1931), dealing with species crosses, finds the F_1 lower than either parent in nicotine content and transgressive inheritance in the F_2.

It is clear from this brief summary of present knowledge of the genetical constitution of the tobacco plant, that improvement by any simple application of this knowledge is hardly possible. The genetical differences between the diverse strains are so subtle that purity can only be determined by a comparison of sister plants grown under a range of different environmental conditions. Other methods more suited to the circumstances have to be employed in practice, and the experience in the Netherlands East Indies, which has been reviewed by Tollenaar and Middelburgh (1930) is of considerable interest in this respect. Before protection of the flowers was adopted in the process of raising seed, a certain amount of natural crossing between the various types grown must have occurred, and, as the result of the variability so introduced, a number of local races became established. In these a sufficient degree of homozygosity existed to cause them to appear uniform. At the beginning of the century the practice of protecting the inflorescences was introduced by Jensen and Lodewijks, with the result that, by 1925, Welter found several different strains of *Kanari* being grown which were identical in leaf shape and habit, constant in their progeny, but differing in quality characters not identifiable in the field. Similarly Coolhaas found in an outwardly uniform crop of *Kanari* several strains differing in average rapidity of combustion and therefore separated by heritable differences in the chemical composition of the leaf ash. The conclusion drawn by these authors is that the *Kanari* type used by Jensen was homozygous with regard to the characters which were optically determinable in the field, but heterozygous with regard to the characters, optically indeterminable but on which quality depends; that by introducing rigid self-fertilization, he proceeded to build up a number of strains of very varying quality. They emphasise the dangers inherent to the system, adopted by many estates, of allowing employees to select large plants irrespec-

tive of any test for quality, since there is considerable chance of selecting in the reverse direction from that desired and, as the strains become increasingly homozygous, it is the undesirable qualities that tend to become fixed. In the absence of systematic control for quality they would prefer not to select. They draw the further conclusion that selection for quality, inasmuch as this is so largely influenced by environmental conditions, must be decentralized. It may be conveniently noted here that, though persistent inbreeding does not have the marked effect found, for instance, in the maize plant, it is not entirely without effect. Frimmel (1924) found a marked heterotic effect in crossing certain tobaccos and suggested the use of the F_1 in the growing of commercial tobaccos.

On the matter of crossing these authors are equally emphatic. Owing to the large number of genes, the chance of securing a favourable combination of characters is very remote. d'Angremond (1928) introduced a system of back-crossing on to one of the parental types, thus increasing the chance of identifying the favourable plant, but, even so, practical considerations demand that only closely related types should be crossed.

In the production of desirable new strains attention has been directed to the common method of crossing existing types and the subsequent isolation of strains superior to either parent. The difficulties inherent to this practice in the case of tobacco have been sufficiently indicated. There can be few cases similar to that described by East and already cited, and Tollenaar and Middelburgh go so far as to state that the crosses made by Jensen have yielded nothing of value. Considerable attention has, consequently, been directed to the prospect of securing new and valuable forms through the identification of spontaneous mutations. Mutant plants occur with considerable frequency, and reference has been made to certain of the more commonly occurring forms. These have been listed by East (1928) and by Tollenaar and Middelburgh (1930). The number of forms which arise by mutation and have been identified is, however, limited, and there is a definite tendency for each form to be restricted to certain types. In recent years attention has been devoted to the possibility

of stimulating the production of mutations by exposing the buds to irradiation. Goodspeed and Olson (1927) irradiated flower buds of *N. Tabacum* var. *purpurea* and obtained a large number of aberrant plants showing morphological modifications, and the same experience was obtained by Tollenaar and Middelburgh who secured twenty aberrants; and it is noteworthy that a wide range of characters was involved in the modifications. As the result of the study of these twenty plants these observers concluded that in eighteen cases a single factor was involved, in one case two factors, while the last was a constant form. The behaviour of these forms was further tested by crossing with the normal *Kanari* type. From the practical aspect they conclude that it is possible that valuable mutations may arise and that the chances are that any such valuable form will differ in a single factor only and be capable of being readily established.

It may be noted that, in some cases, chromosomal irregularities accompany the mutational change. These phenomena, however, lead too far from the practical field of breeding to be considered in any detail here; they form a link with the large amount of pure research to which the genus *Nicotiana* has been subjected. The great variability of the tobacco plant and its generic allies has rendered them a favourable subject for study from the earliest days and, in recent years, the genus has been subjected to an intensive study, especially by the team of workers at the University of California. Much light has been thrown on such questions as inter-specific sterility and chromosomal behaviour, and a general review, giving in much detail the results of these more general investigations, has been published by East (1928), while later work, including observations on the effect of irradiation, is to be found in the botanical publications of the University of California.

A further point which has considerable importance from the practical aspect, arises in connection with the germination of tobacco seed. In certain races the germination of seed is stimulated by light to which the seed of other races appears indifferent. Associated with this phenomenon is a definite, but racially variable, reaction to changes of temperature during germination.

Preliminary observations on the subject were made by Goodspeed (1919). More recently Honing (1930) has studied the question of the need of light for germination from the genetical aspect. Reciprocal crosses between light needing and indifferent races show a preponderance of the maternal character which is still present, but in reduced intensity, in the F_2. He concludes that there are minor modifying factors affecting the result and a change of plasma effected by the nucleus in the initially recessive (indifferent) parent. The phenomenon is clearly a complex one as yet not fully understood.

The tobacco plant is heir to numerous diseases, and a summary of those found in the Netherland East Indies is given by Jensen (1920). They may be caused by specific organisms, either fungoid or insect, or they may be physiological. Of the latter type is a chlorotic disease which has been shown by Garner and his associates (1923) to be due to magnesium deficiency and to be aggravated by additional supplies of sulphur.

Thielavia basicola Zopf is a fungus causing the *black root rot* of tobacco and is responsible for extensive damage in the American tobacco fields. It has been studied in much detail at the Connecticut Experimental Station, and Morgan and Anderson (1926) who found the attack to be primarily a question of soil acidity, suggested that the best means of attack lay in the control of this soil character. They found that with a *p*H value of 6 or over the disease was almost certain to appear; with the *p*H value between 6 and 5·6, lime should be avoided; between 5·6 and 5, lime was not required; between 5 and 4·6, lime may be added with caution, while below 4·6, the application of lime will be beneficial. Wolf (1929) has studied the occurrence of resistance in different strains of tobacco. While resistant plants occurred in *White Burley*, *Wisconsin Havanna* and *Pennsylvania Broadleaf*, none were noted in shade tobaccos till 1927 when a few apparently immune plants were found in a crop of Cuban shade tobacco. From eighteen plants selfed a relatively immune strain has been raised, but it is an immunity dependent on environmental conditions. Johnson (1930) has investigated the genetical behaviour of the resistant character and finds the F_1 intermediate in its capacity of resistance.

In the F_2 all grades of resistance were found and certain plants, especially among those susceptible, bred true. There appears, thus, to be partial dominance of resistance, but any Mendelian explanation would involve several factors.

The disease named *Black-shank*, caused by the fungus *Phytophthora nicotianæ* Breda de Haan, is widely distributed and the question of breeding immune strains has been investigated by d'Angremond (1919). More recently Tisdale (1929) notes the isolation of a resistant strain of *Big Cuba* tobacco, the quality of which is only mediocre. Attempts have, therefore, been made to convey its resistance to other superior, but susceptible, strains of cigar wrapper tobaccos. In the F_5 of the resistant *Big Cuba* × *Cuban*, better quality with a resistance of 98 per cent. has been obtained, while certain F_3 selections of the cross between two F_3's of the above cross and of *Big Cuba* × *Connecticut Round Tip* have also proved particularly resistant and at the same time of high quality.

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CHAPTER XIII

DRUGS

OPIUM POPPY (*PAPAVER SOMNIFERUM* L.)

This plant is widely grown as a garden plant in temperate countries and, in the cool season, in subtropical and even tropical areas. As an agricultural crop it is grown for its oil, derived from the seed, in South Europe. In the Near East it is grown to meet the demand for medicinal opium and the derivatives thereof, while, in the Far East and to a decreasing extent in India, the drug is produced for smoking. In Central India only is the crop found growing within the tropics, but it is as a cold-weather crop and the cultivation is decreasing.

The plant is too well known to need description. The flowers open in the early morning at which time the stigmata are receptive, while dehiscence of the anthers may precede opening of the flower. Since the light, and abundant pollen is readily transported by wind and, in addition, the flowers are freely visited by bees, cross-fertilisation is common. In fact, self-sterility may occur, but the details of its incidence have not been worked out. In the majority of cases seed is freely obtained when the flower is enclosed in parchment bags. As the result of this cross-fertilization, a normal crop consists of a wide range of forms with numerous hybrids. The number of stable varietal forms is considerable, and these are, as far as studied, completely interfertile. Tahara (1915) has determined the chromosome number as 11, a number which has been confirmed by Ljungdahl (1922, 1924) in the course of his cytological study of the genus and of inter-specific crosses within it. Morphological differences, especially with reference to the petal colour, seed colour and leaf shape, have been studied by Kajanus (1919), Leake and Prasad (1920) and Myake and Imai (1927). Leake and Prasad (1920) note a correlation between flower colour and length of vegetative period.

In its capacity of a yielder of oil the plant does not appear to have been studied. Owing to the war, with its consequent demand for medicinal opium and its derivatives, an intensive study of the plant was made by Annett in India. His work lies outside the scope of the present note, but he and his associates determined the morphine content of a large number of pure races and found a very wide range between the different races. Unfortunately these results are only recorded in MS. They found also (1921) both a seasonal and local variation of the morphine content. Reference to his work in connection with the war problem in India is given by Leake (1931).

One of the major problems connected with its cultivation in India is the susceptibility of the plant to the leaf fungus (*Phytophthora*) and to a fungus (*Rhizoctonia*) which attacks the root. Though the practical solution of this problem was found to lie elsewhere (Leake, 1931), a considerable varietal range of susceptibility to the former disease was found, notably in the greater susceptibility of the Malwa (Central Indian) races.

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CHAPTER XIV

THE TROPICAL CEREALS

MAIZE (*ZEA MAYS* L.)

THE maize, or, as it is called in America, the corn, plant is the sole member of the Gramineous genus *Zea*. The early history of the plant is lost in obscurity. Apparently of Mexican origin, it is known only in its cultivated forms. Its nearest relative is *Euchlæna mexicana* Schrad., between which and maize Collins and Kempton (1920) obtained hybrids. The plant had long been cultivated in America before the discovery of that continent, and its cultivation has since spread throughout the tropical and subtropical areas of the globe. The various theories concerning its origin have been discussed by Collins (1930). It is now the most important of all cereal cultivated crops and, of the world's production, over 70 per cent. is raised in the United States. The Argentine, Brazil, Mexico, south-east Europe, India and South and East Africa are extensive producers on a commercial basis, while, over large areas of Africa, " mealies " derived from maize form the staple food of the indigenous population.

The uses to which maize is put are innumerable, but primarily it is a food plant, the grain of which is used for human consumption. Apart from the roughly ground state in which the grain is used as the food of many indigenous populations, many specialized products are now made, especially in America, for human consumption, though, being deficient in gluten, maize is not adapted to produce bread. By hydrolysis glucose is prepared; by fermentation alcohol in many potable forms and acetic acid are obtained, while, owing to the cheapness of the grain, there exist large potentialities for the production of power alcohol. Fermentation by *Bacterium amylobacter*, yielding butanol and acetone, is being developed on a commercial basis. Large quantities of the

grain are used as a feed for livestock, while both the green and dry stalks are used as fodder, the former being well adapted to form silage. Commercially the stalks find a further use in the paper and rayon trades, and, by pressure, are made into lumber substitutes. With this range of utility, it is the grain that remains the dominant economic product, and the primary effort in all countries is directed to the increase of the yield of grain.

The plant is too well known to merit detailed description. It is a typical gramineous plant which, under favourable conditions, grows rapidly as a single vertical stem attaining a height of 10 feet and over. The root system develops from the lowest nodes of the stem both below and above ground level. The plant is monoecious with diclinous flowers, the male and female flowers being carried on separate inflorescences. Exceptionally male flowers appear on female inflorescences and *vice versâ.* Variations from the normal distribution have been studied by Jones (1930) and Schaffner (1930); the latter finds that the male inflorescence is modified by photo-periodic influences. The male inflorescence is terminal and forms a loose panicle, the tassel. The flowers are paired on short spikelets, themselves paired, situated on the axis and branches of the panicle. The anthers of the three stamens are bilobed and carried on long, pendent filaments. Dehiscence takes place through short slits at the distal end. The entire structure of the inflorescence is adapted for wind pollination. The viability of the pollen is low; after twenty hours it rapidly declines and pollen forty-eight to sixty hours old has been shown by Kiesselbach (1922) to be functionless.

The female inflorescence is a dense spike, the ear, carried laterally and developing from a bud borne in a leaf axil of the main stem. The branch terminating in the inflorescence is much compressed. The leaves arising from the lower nodes are modified to form the husk which envelops the spike closely. The upper nodes are still further compressed as well as swollen to form the axis of the spike itself, the cob. The paired flowers are borne on paired sessile spikelets situated on the cob. Normally only one flower of each spikelet develops and the grains are, therefore,

arranged in longitudinal rows which form a multiple of two and are usually eight or over. The stigma is not differentiated from the style and together they form the "silk." The silks are receptive even before they protrude from the husk and they remain receptive from ten to twenty-one days. By gradual elongation they are extruded and may attain a length of 24 inches, but growth is checked as the result of pollination. The tip is usually cleft, while the surface, especially at the distal end, is covered with short, branched hairs. Again, the entire structure of the silk is well adapted to wind fertilization.

In addition to structure and the disposition of the sexes in separate inflorescences, a further guarantee of cross-fertilization is found in dichogamy. Though a few varieties are protogynous, the majority are protandrous. The extent to which the one sex anticipates the other is, however, subject to marked fluctuations due to weather; warm weather stimulating the development of the male flowers and cool, damp weather the development of the female flowers. The entire reproductive organization is thus designed to ensure cross-fertilization which is the rule.

The grain is composed of a tough outer coat, the pericarp, formed by the fusion of the ovarian wall with the testa; within lies the endosperm with an outer aleurone layer. The embryo is situated marginally with the scutellum closely appressed to the endosperm.

As the result of long-continued cultivation under different conditions, innumerable varieties have been developed, but such varieties have not the definiteness which accompanies the term when applied to plants which are normally self-fertilized. These varieties fall into certain well-defined groups, distinguished mainly by their grain characteristics. These groups have been described by Sturtevant (1920), and the more important, in the economic sense, are :—

Var. *indentata*. Dent maize. The typical dent in the crown of the grain is due to the shrinkage of the starchy endosperm which lies between two layers of corneous endosperm. It is a maize of much importance in South Africa.

Var. *indurata*. Flint maize. The corneous endosperm forms a

continuous layer over the starchy endosperm. It is a maize widely grown in the Argentine and in south Europe.

Var. *saccharata*. Sweet maize. The endosperm contains sugar instead of starch and the translucent grain wrinkles on drying. It is mainly used as a vegetable or for canning.

Var. *amylacea*. Flour, or soft, maize. The corneous endosperm is absent and the grain is soft.

Var. *everta*. Pop maize. The endosperm is corneous throughout, and, in consequence, the grain gives the characteristic pop when heated.

The numerous and frequently named varieties within these groups have no definite entity. They are types conforming to the particular standard set by the breeder and maintained to that standard by selection. Transferred to other conditions and with selection to that set standard no longer enforced, they soon cease to conform and, in consequence, the same name will frequently be found applied to very different types.

In the past, and very largely at the present time, a selection based solely on appearance is used when corn is set aside for "seed." This is the case even in the United States, where an attention has been devoted to the crop which is equal to its importance in the agricultural economy of that country. It is by such means that the numerous varieties, of which over a thousand are recorded, have been produced. That considerable improvement is possible by such means is beyond question, but this is a generalized statement which requires a more critical definition. Nearly fifty years ago Mueller (1886) showed to what extent a character such as the number of rows on the cob could be altered by the mere process of selecting in each generation the ears bearing the greatest number of rows. A similar experiment was carried out by de Vries (1900), who, starting with a race of maize of which the average number of rows varied between twelve and fourteen, in five years raised a race with a mean of twenty rows at which number the race was maintained for seven years. Subsequent selection within this race for ears with the smallest number of rows reduced the average number of rows to that of the original race in three years. Mass selection is thus a

means of improvement in a low-bred race, but its main function in practice is less improvement than maintenance of a standard already attained. Nevertheless, much work has been done with the object of rendering mass selection more effective in maize. This work, which is mainly directed to the identification of characters associated with high yield, that primary desideratum of the corn grower, has been summarized by Richey (1927). The evidence is mainly concerned with ear characters, and the comparisons favour ears which are heavy because they are long, as opposed to ears which are heavy because of a larger circumference. Ears with heavier cobs, fewer rows, fewer kernels per inch in the row and with a lower shelling percentage are generally associated with heavy yield. Of plant, as opposed to ear characters, capacity to bear two ears appears to be associated with heavy yield; otherwise adaptation to locality, or, in other words, general vigour, is the most important character.

An advance on mass selection is found in the method known as "ear to row" selection introduced at the Illinois Agricultural Experiment Station in 1896. Essentially it is a method of evaluating parental potentiality through the offspring. Each row is planted with grain from a single selected ear and the potentiality of the parent judged from the regularity of the offspring in the row. The method has many variant forms designed to discount extraneous influences such as variations in the soil, but the basic principle remains the same. As an example of what may be achieved by this method the case of *Burr White* may be instanced. *Burr White* maize has a normal oil content of 4·70 per cent. and a protein content of 10·92 per cent. Selection with the object of raising, as well as lowering, the percentage content of these two constituents was carried out with the result that the oil content was changed in the one direction to 8·02, and, in the other, to 2·03, while the protein content was similarly altered to 14·53 and 7·74. The improvements which have been effected by these methods, however, refer more particularly to specific characters other than yield (Richey, *loc. cit.*).

Further advance awaited more precise knowledge of the genetic constitution of the maize plant and considerable progress has

been made in recent years as the result of the large volume of work which these years have witnessed. Since the maize plant is habitually cross-fertilized, each parent race consists of an aggregate of individuals of different gametic constitution and pure only with regard to the major characteristics. Purity in respect of those elusive and indefinite characters which go to build up yield is unobtainable in practice by any method of selection which takes into account one parent only, as is the case where open fertilization is permitted. The simplest method, and that commonly adopted for the establishment of purity, is inbreeding, or the fertilization by pollen of the same, or a sister plant. In maize, however, this method is ruled out; for, every time ordinary varieties have been self-fertilized, a diminution of growth has taken place (Jones, 1917). Nevertheless, it is by modification of this method that the most recent advances in maize breeding have been effected.

The ease with which the maize plant could be grown, the readiness with which fertilization could be controlled and the abundant supply of grain harvested, were reasons which led to its adoption in the early investigations on inheritance which followed the discovery of Mendel's work. Of such a nature are the investigations of Correns (1899) and Lock (1912); but it is the importance of the maize crop in the United States which has led to the vast amount of study which has been devoted to the plant in recent years.

The maize plant normally possesses 20 chromosomes (Fisk, 1925), though Kuwada (1915) found the number to vary from 20 to 22, and aberrant forms have been found by Fisk in *Black Mexican* sweet maize and by others in later investigations (Langley, 1927; McClintock, 1929a; Randolph, 1928). With the advance of knowledge, records of the departure from the normal chromosome formation are becoming more frequent; McClintock (1929b) has studied a triploid form, while Burnham (1930) has found an association at meiosis of non-homologous chromosomes, producing linkage between factors generally independent, a phenomenon which has been found to occur in other plants, notably *Pisum*, and which is apparently the cause of the different forms of semi-sterility already identified. These chromosomal investiga-

tions have now reached a degree of complexity second only to those on *Drosophila*, and they have an important bearing on general theoretical problems into which it is not possible to enter here.

To date, more than 180 genes have been identified, and, since the haploid chromosome number is only 10, it would be anticipated that the phenomenon of linkage would be in evidence. This expectation has been fulfilled; the first case of linkage, that between waxy and coloured endosperm, was reported by Collins and Kempton (1912), and recent years have seen rapid progress in the unravelling of the genetic constitution of the maize plant. Already nine linkage groups have been definitely established, while Anderson and Emerson (1931) have studied a chocolate pericarp colour, a simple dominant to colourless, which shows no indication of linkage with any of the nine known groups and represents, therefore, in all probability the tenth group. In the recent volumes of the *Journal of Heredity* are to be found an extensive series of papers dealing with examples of linkage in maize and the position of recent knowledge has been reviewed by Lindstrom (1930), who (1929) has also recorded linkage between certain quantitative and qualitative characters, particularly between number of rows and aleurone and endosperm colour as well as endosperm texture (sugary endosperm). Chlorophyll is controlled by at least 67 genes, plant height by 8, aleurone colour by 10 and endosperm development by at least 16, in addition to the 8 which determine the main characters, sugary, waxy flint, and so on. There is no evidence to indicate that any one chromosome carries most, or all, of the genes of a special plant character. On the contrary, there appears to be a random distribution of genes. Thus :—

Genes	determining	general height	occupy	5	different	chromosomes
,,	,,	leaf variations	,,	5	,,	,,
,,	,,	inflorescence	,,	5	,,	,,
,,	,,	embryo	,,	3	,,	,,
,,	,,	endosperm	,,	4	,,	,,
,,	,,	chlorophyll	,,	9	,,	,,
,,	,,	anthocyanin and flavone.	,,	8	,,	,,

Progress, as is natural, has been greatest where qualitative characters have formed the subject of study, and in few cases do these concern yield, though exceptions to this statement are to be found in such factors as sterility, chlorophyll deficiency and certain lethal factors. Other phenomena which add complexity to the analysis may be mentioned at this point. In certain cases, notably in a cross between a sweet corn and a pop corn, a deficiency of sugary grains is found to occur. This has been attributed by Jones (1922b) to a differential rate of growth of the pollen tubes, but the problem is hardly so simple, as the later work of Mangelsdorf (1929) on the relation between stylar length and Mendelian segregation indicates. Kempton (1927), again, has noted a change of Mendelian ratio induced by age of pollen.

A further phenomenon of some interest is that known as male sterility which was noticed by Eyster (1921). A similar, and possibly identical, case was observed by Singleton and Jones (1930) in which the anthers fail to extrude and contain no pollen. The phenomenon is apparently connected with the failure of the nucleus to go through the first microspore division and the character is controlled by a single factor. The female organs are normal and the advantage of the character in one parent when raising crossed grain for commercial purposes is obvious. Demerec (1929) has investigated a case of cross-sterility of another kind. While studying the inheritance of albinism, he found a rice-pop corn which failed to set seed when it was used as the female parent, though when used as the male parent the set of seed was perfect. This cross-sterility is not fully explained, but appears to be connected with that deficiency of sugary classes to which reference has already been made.

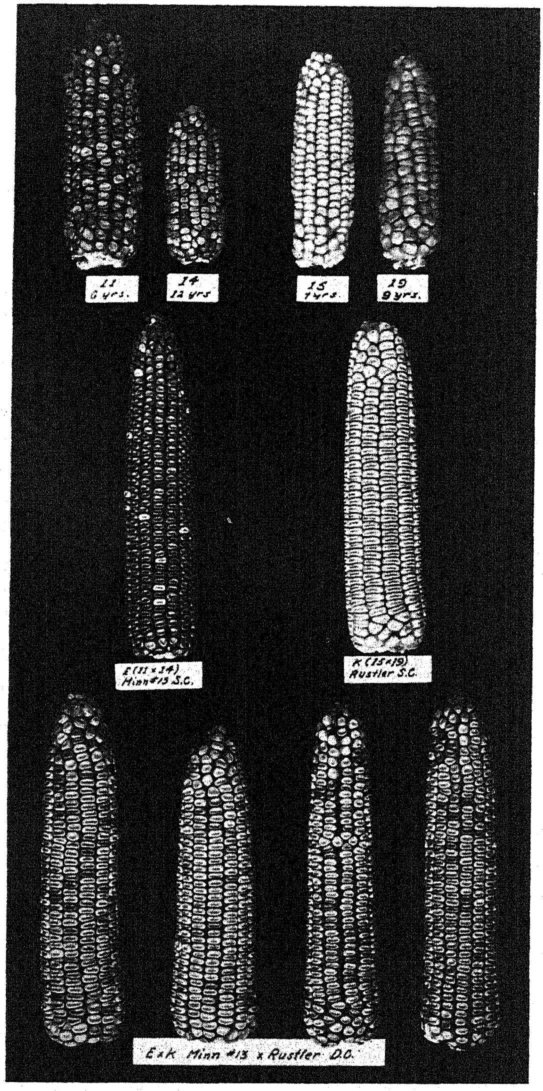
As the result of the detailed investigation to which the maize plant has been subjected, the number of mutational forms which have been identified is considerable and, in fact, many of those characters of which the factorial basis has been worked out have arisen in this manner. More recently the possibility of inducing mutational change by irradiation has been studied in maize by methods similar to those adopted in work of a like nature in other plants, notably tobacco. Irradiation has been applied both to

the pollen and to the fertilized gametes, and the chromosomal effects studied in a large number of cases. The induced changes may take the form of actual disjunction of the chromosomes or merely affect the individual genes leading to the production of recessive mutations. Available knowledge of the latter phenomena has been recently reviewed by Stadler (1931). As in other cases in which the effect of irradiation has been investigated, the number of mutational changes has been increased, but the application of the method has been used mainly to throw light on the physical nature of the phenomena accompanying mutation, a problem lying within the field of pure research.

Early in the genetic study of the maize plant, when those characters which concern the grain and have, therefore, an economic significance, were chiefly under consideration, a source of complexity was soon discovered. The grain of the maize plant is albuminous and the major portion of it is formed by the endosperm. In this endosperm, as the direct result of a cross, appear characters which are derived from the pollen parent. This phenomenon, to which Focke applied the term "Xenia," was observed by Correns (1899), and, following Nawaschin's discovery (1899) that a fusion takes place between one of the sperm nuclei and the primary endosperm nucleus, itself formed by the fusion of the two polar nuclei, Guignard (1901) identified this fusion in maize. This phenomenon of double fertilization in maize has been studied repeatedly (East, 1913) and is discussed by Weatherwax in a series of papers (1916–1919) dealing with the morphology and development of the flower. The characters displayed by the tissues derived from the endosperm require, therefore, special interpretation, for they result from the interaction, on fusion, of three nuclei, two of female and one of male origin.

A further phenomenon which receives prominent demonstration in maize is that of heterosis or hybrid vigour. As has already been noted, it has not been found practicable to raise commercial varieties by the direct process of self-fertilization, for a diminution of growth takes place which is sufficient to render all selfed strains unremunerative. There is here at work a process which is the

PLATE XII



Zea Mays L. *Top:* The four selfed lines; *Middle:* First generation crosses; *Below:* The double cross.

By courtesy of Dr. H. K. Hayes. *Reproduced from " Univ. Minn., Agric. Expt. Sta., Bull. 275."*

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reverse of heterosis, an elimination of those characters which are responsible for the vigour which all commercial varieties, being a mixture of heterozygous forms, possess. The modern concept of heterosis brings the phenomenon into line with other genetic phenomena, and, under this concept, vigour is the expression of the interaction of a number of particulate genes. The phenomenon as exhibited in maize has been discussed by East and Hayes (1912) and by numerous other investigators in more recent times, but it is a phenomenon which is complicated by linkage which is found to affect the characters responsible (Jones, 1917). On the one hand, the large amount of study devoted to the phenomenon in maize has a wide theoretical application in problems connected with the relative survival chances of dominant and recessive mutations, a subject which has been discussed in its mathematical aspect by Fisher (1930); on the other, it has a direct bearing on the practical question of crop improvement.

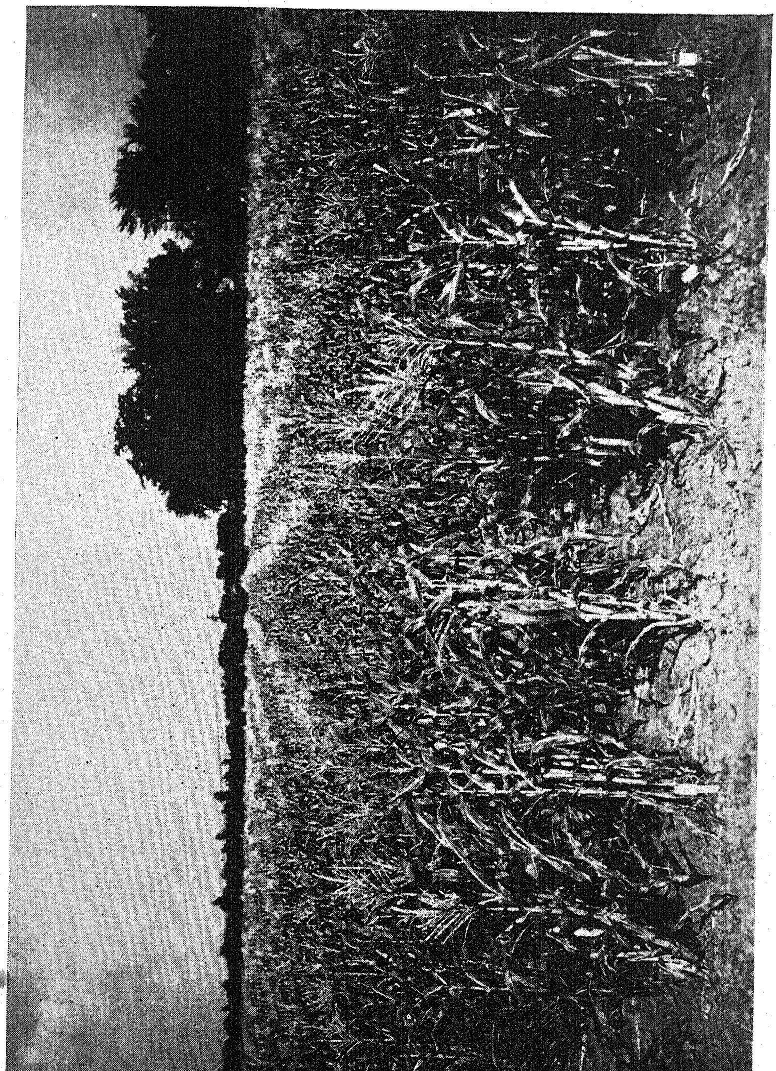
In the plants composing a commercial variety, many of the factors which react on vigour will occur in the heterozygous condition, and the result of inbreeding will be the production of a number of strains with a progressive increase in the number of homozygous factors. Such a process has a double effect. In the first place, it leads to a separation of factors on whose combined presence full vigour depends; in the second, it eliminates rapidly, and in the course of a few generations, those simpler and more obvious forms of reduced vigour which are due to recessive factors. Of such a nature are the factors producing dwarfness, sterility and chlorophyll deficiency, of which a number is known. As the result of selfing, a number of strains is obtained which, though showing reduced vigour, and, therefore, themselves of no commercial value, will be free from the grosser defects to which the maize plant is heir. If now two such strains be intercrossed, a recombination of factors imparting vigour may be obtained; and a judicious selection of selfed parental strains will yield an F_1 possessing a vigour even in excess of the original variety. Such increase was early noticed by Shull (1908–1911), and a more recent study has been made by Richey and Mayer (1925). Difficulties, however, arise in the practical application of the principle

owing to the necessity of maintaining the parental stock of selfed lines from which the amount of grain obtained is relatively small owing to the diminished vigour of these plants.

A further step in the application of the modern interpretation of heterosis to practical problems was taken in the double cross. In the double cross the two F_1's, derived from two pairs of selfed strains, are crossed *inter se*, thereby not only increasing the chance of securing a combination of desirable characters, but securing also the additional advantage that the F_1 parental stock, having the vigour of a cross, will yield a full crop of well-developed grain. By this means the work commenced by East and Hayes resulted in the *Burr-Leaming* double cross which, over a succession of years, yielded an increase of 27·5 per cent. Further studies of the method have been made by Jones (1922) and other workers, while the commercial application of the method in Minnesota has been discussed by Hayes and his associates (1931). Garber (1931) gives the area under the double cross as 30,000 acres with an average increased yield of 10 per cent. Kiesselbach (1922) has shown that more advanced generations than the F_1 may be used for the purpose of raising double crosses without appreciable effect on yield. Hayes and Garber (1919) have suggested as a modified method, the synthesis of a stable race by intercrossing a sufficient number of selfed lines, and the method has been applied by Richey in the case of *Delta Prolific*. Still later Lindstrom (1931) has indicated yet another method of securing the practical advantage of the double cross. Here the pollen parent alone is inbred and planted in an isolated field of a standard variety, all the plants of which are detasseled. Not only is a bulk of seed obtained of which the male parentage is definitely known, but seed of the inbred sire is also obtained in a condition of purity with the minimum of effort. Success results from a correct choice of standard variety and male parent, a choice which is a matter for experiment, but Lindstrom has succeeded in securing increases up to 50 per cent. as the result of such choice.

Essentially the process here involved consists of the elimination, by inbreeding, of the more prominent factors which adversely

PLATE XIII



Zea Mays L. Producing double-crossed seed; two rows female parent, detasseled, grown between single rows of the male parent.

By courtesy of Dr. H. K. Hayes.

Reproduced from "Univ. Minn., Agric. Expt. Sta., Bull. 275."

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affect yield and, by subsequent recombination, the building up of a plant possessing a full complement of favourable factors. Some of the adverse factors are readily identified, for their effect is definite and, in extreme cases, lethal. But others, as yet indefinite in number, are less easily identified, and, in the present state of knowledge, the desirable recombination is only to be found by a process of trial and error. It must be noted that a race, possessing a sufficiency of advantageous factors in the homozygous condition and, therefore, possessing the full vigour associated with the term heterosis, is a theoretical possibility; but, in view of the large number of factors apparently involved, the probability of its isolation is very remote, while any direct attempt to secure it must await more adequate knowledge of those factors. Collateral work has been directed mainly to an attempt to find parental characters which, in the selfed strain, are correlated with high yield in the single or double cross (Jenkins, 1924).

The question of hybrid vigour in maize has been approached from a different angle by Ashby (1930). He finds from a calculation of the growth rate that the hybrid does not differ from its more vigorous parent as regards relative growth rate nor from either parent as regards cell size, photosynthetic efficiency of leaves or time of flattening of the sigmoid curve. The only physiological differences observed were increased percentage of germination on the part of the hybrid and also a greater initial weight of the embryo which gave an advantage which was maintained throughout the period of growth. He found, further, that the relative growth rate was apparently inherited. A recent discussion of the practical problems raised by the utilization of inbred strains of maize is that of Brink (1930). He points out that the supreme merit of the system lies in the opportunity it affords for eliminating undesirable genes and that the ultimate objective lies beyond the stage when high yield is only to be obtained in a hybrid between two strains; it lies in the production of a self-perpetuating high yielding strain.

Greatest attention has hitherto been paid to the question of yield and few other qualitative characters have received any

considerable attention. Hayes (1922) has succeeded in raising the protein content by intercrossing selfed lines, themselves selected for high protein content. A certain amount of work, too, has been done by Hauge and Trost (1928, 1930) on the inheritance of vitamin A in the grain of maize. Using the ophthalmic test, these authors have found that the vitamin A content of dent maize is controlled by a simple factor, and that the genes are the same as those governing the development of the yellow colour of the endosperm.

Of importance second only to the question of inherent capacity to yield, is the question of disease; for disease will prevent such inherent capacity from expressing itself in the crop. The maize plant is subject to numerous diseases, many of which have not been studied from this aspect; but in certain cases, as has generally been found, different races and strains have been identified as possessing different degrees of susceptibility. The subject, in its bearing on the maize plant, has been discussed by Jones (1918).

One of the more important diseases is that produced by *Ustilago Maydis* (D.C.) Tul., a "Smut" fungus widely distributed in maize-growing countries. Jones' work on this disease has been extended by Hayes and his colleagues (1924), Garber and Quisenberry (1925) and by Immer (1927), who was able to show that resistance was transmitted by either parent and to trace out certain linkage relations. Ranker (1930) finds a soluble substance in the tissue juice of resistant strains which is apparently equally effective for the several physiological forms of the fungus known to exist (Stakman, 1929). He finds, further, that the substance is not invariably present in resistant strains, so that there appear to be other bases for immunity.

The incidence of *Puccinia sorghi* Schw. (*P. Maydis* Bér.) has been investigated by Stakman and his associates (1928). They find seven physiological races of the fungus to which selfed strains respond differently. Mains (1928) finds, for two of the physiological forms, that resistance is controlled by a single factor for which he identified no linkage relationships.

Two further fungoid diseases of considerable importance and wide distribution have been studied from the same aspect.

Gibberella saubinettii (Mont.) Sacc., the cause of *Pink Rot*, has been studied by Dickson and Holbert (1926), especially with respect to temperature effect. At low temperatures (8° to 10° C.) seedlings are relatively low in soluble carbohydrate-building substances, principally dextrose, sucrose and hexoses, and have their cell walls composed of pentosan-yielding substances; at high temperatures they have large reserves of soluble carbohydrate-building substances, principally sucrose, glucose and fructose, and have cell walls impregnated with suberin. Each self-pollinated line has been found to have very definite temperature limits within which it is capable of resisting disease, and disease resistance is an inherited character the operation of which is constant over a given range of temperatures for each strain. The F_1 hybrid, susceptible by resistant, is susceptible. Hoppe (1929) has made a further study of the inheritance of this resistance. *Aplanobacter Stewartii* E. F. S., the cause of Stewart's disease in sweet maize, and a bacterial " wilt," has also been studied. Reddy and Holbert (1928) find in this case that resistance varies in different strains, but is not correlated with vegetative vigour.

Of insect pests, the corn-borer (*Pyrausta nubilalis* Hübn.), is widely distributed and is spreading in the United States. Certain varieties of maize have been known to be resistant. Roubaud (1928) reports complete immunity for *Dent de Cheval* and partial immunity for *Hatif d'Auxonne* in France, and a similar report is given for *Pferdzahn* in Germany by Hase (1927). Marston (1930) made use of the resistant South American maize *Amargo*, a form too late for Michigan, and raised F_3 families which were completely resistant. Resistance appeared to be a simple Mendelian factor, the association of which with any external plant character was not identified.

Of a different nature is the susceptibility to the *Earworm* (*Chloridea obsoleta* Fab.). Here the susceptibility is definitely associated with specific varietal characters. Collins and Kempton (1917) have succeeded in securing a partial immunity by an increase of the length and thickness of the husk and by a reduction in the number of husk leaves. Work on the inheritance of resistance to disease is yet in its infancy in respect to maize, but

it already promises to afford a valuable line of attack which will have important economic results.

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RICE (*ORYZA SATIVA* L.)

Statistical statements of area and outturn of crops which are widely cultivated by the more primitive races, are necessarily

little more than rough approximations, and if available statistics give to maize the credit of being the most widely cultivated of all crops, to rice must be given the credit of being the most important source of human food. The cultivation of rice dates from prehistoric times and, as with so many of the older plants of cultivation, the wild plant from which it has been derived, and even its country of origin, are not definitely known. Wild rices, so called, are found in many countries, but it is far from certain that these are not escapes. In spite of the presence of such wild rices in South America, the evidence points to south-east Asia as being most probably the home of the wild plant. Essentially, rice is a tropical plant, growing in the humid lowlands, but its cultivation has spread far beyond the limits of the tropics proper. It is grown as far north as Spain, Italy, Japan and in America, California, while in India the " mountain rices " grow in the Himalayas up to 6,000 feet.

The most characteristic feature of the rice plant is a physiological one, its relationship to water. Though at one extreme the cultivation of mountain rices approximates to that of the temperate cereals, even for these an abundant and well-distributed rainfall is essential. Moreover, these are exceptional and most rices require a water supply which leaves water standing on the field. On steep slopes, such as are used for the cultivation of rice in Ceylon and the Philippines as well as elsewhere, the extensive terracing which is so characteristic a feature of those countries, permits the flow of water from terrace to terrace, while low embankments retain the water on each terrace. In the lowlands, as of Burma and Bengal, it is the flood water from the rivers which submerges the land and gives the necessary supply. At the other extreme are the deep-water rices of Bengal which grow on the swampy lands left, after the floods have subsided, with a covering of water as much as 5 to 6 feet deep. This physiological adaptation is associated with peculiarities of root structure and development which have been studied by Sethi (1930).

Rice forms the staple diet of the populations of many of those countries in which it grows, and a large volume of the crop never comes on to the market. Much of the trade in rice, too, is directed

to supply countries such as Japan, Java and Ceylon which, though themselves large producers, do not satisfy their requirements by home production. Among the temperate races for whom rice does not form the staple diet, quality is largely determined by an appearance due, in the first instance, to varietal differences of shape of grain, but even more to the preparatory processes, grouped under the general term of milling, to which the rice as harvested is subjected. To the grower, therefore, the primary consideration is yield, but he should pay attention to such points as evenness in size of grain, points which are of importance to the miller and for which the miller is prepared to pay a premium.

With the exception of *O. longistaminata* Chev. and Roehr., a perennial plant spreading by underground rhizomes and to a small extent cultivated in equatorial Africa, the entire range of cultivated rices belong to the single species *O. sativa* L. They are, like other cultivated cereals, annual grasses frequently maturing very rapidly. During the vegetative stage tillers are developed, and from the terminal buds of these the ears arise. The inflorescence is a loose panicle, the branches of which arise singly or in whorls, and may themselves branch. Each ultimate branch carries a number of spikelets, and each spikelet is composed of a single flower with its extra-floral organs. The flower proper consists of two laterally placed lodicules, six stamens and an ovary terminating in two long plumose sessile styles. The extra-floral organs consist of two small outer glumes and, above these, the floral glumes, two in number and called respectively the palea and lemma. The distal flowers of the main axis and of each branch are the first to mature and flowering proceeds progressively downwards. At the moment of blooming the floral glumes are forced apart by the swelling lodicules and the anthers are extruded. After a short period, which may be reckoned in minutes, the floral glumes close on each other and ultimately fuse to form the hull. Pollination has been studied by numerous observers, and is found to take place normally just before, or at the moment when the flower opens, though occasionally it may be delayed till the flower has opened. These observations are not in full accord and it seems probable that there is a varietal divergence in the exact sequence; there is

undoubtedly a differential response to environmental conditions. Observations on the extent to which natural cross-fertilization takes place harmonize with the above conclusion. Most of these observations indicate a low percentage of crosses. Akemine and Nakamura (1925), for instance, as the result of extensive experiments, found a racial difference varying from 2·32 per cent. in *Sasaki* rice to 0·21 in *Kuromochi*. These are only the observed crosses when the varieties were grown in alternate lines, and necessarily give an underestimate of the total number of offspring resulting from cross-fertilization. He found, too, the amount of cross-fertilization to be largely influenced by environmental conditions which affected the time of shedding of the pollen. In Java alone has the observed amount of cross-fertilization largely exceeded these figures, rising as high as 25 per cent., and Heide (1923) is led to classify the rices into three groups according as they have open pollination, variable pollination dependent on climatological factors or closed pollination. To the divergence in the varieties studied and in the environmental conditions under which those studies were conducted must be traced the lack of accord above noted. Similar differences occur in the observations on the time of opening of the flower. Usually this occurs about 7 a.m. to 10 a.m., but there is a seasonal variation in the hour of opening at any one locality which harmonizes with the later hours found in northern latitudes as in Japan and California. These observations suggest that, apart from varietal differences, temperature is one of the major factors influencing the opening of the flowers. Studies of the influence of the various factors of the environment on the details of flowering in their various aspects have been made by Noguchi (Kobyasi) (1926–1931). Much work remains to be done in unravelling the details of fertilization and especially of the viability of pollen, but one general conclusion can be drawn from these observations. It is necessary to determine for each locality as well as for each variety the extent to which natural cross-fertilization takes place before breeding work can be undertaken.

The number of varieties of rice has never been determined with certainty. It is a crop developed by, and practically confined to,

peasant cultivation where each cultivator normally furnishes his own seed supply. These are conditions which, in a crop covering such a wide area and occupying such diverse countries, make for local varieties. The number of varieties bearing local names is legion, but such varietal distinctions lack scientific significance. The number, however, making all due allowances, probably exceeds a thousand. The earliest studies of the plant not unnaturally gave predominance to the morphological characters of that portion of the plant which was most widely known, namely, the grain. Such a classification is that of Koernicke (1885) which separates the so-called glutinous rices from the common rices, groups the latter into awned and awnless forms and subdivides these according to the shape of the grain and the colour of the hull. It is a purely morphological classification and, from the practical aspect, it is the agricultural characteristics which are of predominant importance. Kikkawa (1912) has added a classification based on agricultural characteristics and the analyses of the types of rice grown in different localities are now numerous. The importance of a consideration of the agricultural characteristics rests in the fact that physiological adaptation has proceeded further in rice than in any other agricultural plant. In Malaya and Burma, where rice is grown on inundated lands, a difference of field level of only a few inches which affects not only the depth of water, but the length of season, involves a varietal difference in the crop. This adaptation is carried still further in Bengal where, in addition to the above adaptations, a seasonal adaptation also occurs. Here the main agricultural classes are :—

Aus—Highland rice. Standing water is not required. Sown broadcast in April to May and reaped in July to September.

Aman—Transplanted winter rice. Sown in June to July; transplanted into standing water July to August and harvested October to January.

Aus—Lowland rice. Sown broadcast in February to March on the first showers on low lands which subsequently become inundated. Harvested in July to September in standing water up to 5 to 6 feet.

Aman—Lowland rice. Sown broadcast on lands still lower than the last and continuing growth till November to January. The water may attain a depth of 30 feet.

Boro—Spring rice. Sown about October and transplanted in January on muddy banks following the retreating flood and on the lowest lands which do not dry out. Usually planted where irrigation facilities are available.

Hector (1930), from whose account the above classification is abbreviated, brings out very clearly the point that, as far as morphological characters are concerned, many varieties of one of the above groups are indistinguishable from varieties of another group. In all countries it is the varieties of the first two groups which supply the bulk of the crop and these, therefore, are the most important. It is on them that most of the investigations on rice have been conducted.

The question of the classification of the rices has been carried a stage further by the recent work of Kato and his colleagues (1930). They have distinguished two types of rice which they call *japonica* and *indica* respectively. The former are indigenous to Japan and Korea, the latter to south China, India and Java, etc., and they thus form a natural division between the more truly tropical and the temperate forms. But the distinction goes deeper and has a cytological basis. While varieties within these two types are mutually inter-fertile, hybrids between the two types are much less fertile owing to the formation of many imperfect pollen grains, and the difference in grade of sexual affinity is demonstrable by sero-diagnostic reactions. Jones (1930), too, working with Chinese and Japanese races, found a high degree of sterility in the F_1 of certain crosses and deduced from the evidence the existence of chromosomal incompatibility. Cytological investigations on the nuclear structure of the rice plant were first undertaken by Kuwada (1910), who found the haploid number to be twelve. This result has been confirmed by several later investigators, notably by Nakatomi (1923) in Japan and Rau (1929) in India, the former of whom found a varietal difference in size of chromosomes. Selim (1930), working on five races of rice covering both Kato's types, has found that, although these five races have

the same sized nuclei and the same number of chromosomes, yet they differ characteristically in the nuclear content of the pollen mother cells. The cytological phenomena of the rice plant clearly require further detailed study before they can offer a clear basis for varietal classification.

In spite of the high physiological specialization of the plant, the varieties of rice as usually grown consist of mixtures owing to the occurrence of natural cross-fertilization and of mechanical mixing which the cultivation of a number of varieties in one locality renders almost inevitable. The effect of these will, in part, be counteracted by that very specialization but in some countries a certain degree of purity is maintained by a deliberate, though rough, mass selection. Either separate harvesting of heads for seed purposes is undertaken or the selection may be made in the bundle. These methods are adopted by the peasant rice grower in many countries (Mitra, 1922). Mass selection on a well-organized basis is responsible for the high degree of purity and the yields obtained in Italy and Spain, and in this organization, the Vercelli station has played a preponderating *rôle*. Elsewhere, and especially in the home of rice, the work of varietal classification has been associated with the isolation and multiplication of pure strains. The " plant to row " method, modified to suit particular conditions, has resulted in the production of a number of strains in the United States (Chambliss and Jenkins, 1923). In India Finlow (1917) has given an account of the selection by Hector in Bengal of the *Indrasail* strain now so widely grown in that tract, and Bhide and Bhalerao (1927) note the isolation of numerous strains of *Kolambe* rice, a rice grown in the northern Konkan which, though of good quality, was unacceptable to millers owing to the variable size of the grain. In Ceylon Lord (1929) has conducted similar work, paying special attention to the comparative methods for testing the selected varieties. In Java the results of selection have not been comparable with those obtained elsewhere, and the reasons appear to be, firstly, the extent of natural cross-fertilization found to occur and apparently peculiar to Java; secondly, the centralization of the early selection work which paid insufficient attention to the intense physiological specializa-

tion of the plant; thirdly, to the absence of an organization for seed distribution which would maintain purity. The entire system has now been reorganized and an account of that now adopted has been given by Koch (1929). The work of Jack (1923) in Malaya has been reviewed by Sands (1924), who again emphasizes the fact, arising out of the physiological specialization of the rice plant, that it is necessary to isolate a wide range of strains and to work with more than one variety. The scope of improvement through the isolation and introduction of pure strains, as the progress already attained shows, is considerable, but the practical benefits will be slow in coming to fruition owing to the difficulties inherent in the problem of organizing a seed supply among an unorganized peasantry with miniature holdings.

Yield being the primary consideration in rice production, efforts have been made to trace a correlation between yield and some other character of the plant by which it would be possible to identify and isolate the most desirable type of plant with greater certainty than is possible by the measurement of yield itself which responds so readily to environmental influences. For, besides the edaphic influences which may be eliminated by a suitable scheme of plots, great differences in the growth and production of rice occur, as Peralta (1919) has shown, from planting rice at different seasons, a fact which may be associated with the photoperiodic action referred to below. A large number of correlations has been determined by Jacobson (1916) and Vibar (1921), who found a marked correlation between yield on the one hand and tillering and days to maturity on the other; to a lesser extent, between yield and length of culm, length of panicle, number of nodes in the panicle and length of grain. A further study has been made by Kondo and Nogati (1922), and these authors conclude that it is impossible to select a heavy yielder through any other character than yield itself. Of special interest, however, in view of Vibar's work, is Jones' observation (1928) that, in the crosses studied by him, there is no interdependence between yield and earliness and that it is possible to combine the two characters in a single plant.

The photoperiodic action to which reference is made above,

was noted by Hara (1930). Fuke (1931) has studied the question further and found that limitation of illumination to the hours from 8 a.m. to 4 p.m. caused the plant to head out earlier than normal and that a greater response was obtained when the treatment was applied early in the growth period. Similarly, prolongation of the exposure to light delayed heading out. Noguchi (1930) found that the same effect was obtained when the application of the short day was limited to twenty days early in the life of the plant and not continued till heading out occurred. These observations have a bearing on the varietal differences associated with races grown at very different latitudes.

Work on the genetic constitution of the rice plant is all of comparatively recent date and the difficulty which meets any attempt to correlate the observations of the now numerous investigators lies very largely in the fact that they are drawn from experiments with widely different varieties. The earliest investigations are those of van de Stok, and his results are summarized by him in Fruwirth's Die Zuchtung der landw. Kulturpf. (1912). Subsequently followed those of Hector and Parnell in India. In the last ten years an immense amount of work has been conducted in Japan and, latterly, in the United States in connection with the development of rice cultivation in California. In 1927 Ikeno published a somewhat detailed summary of the information at that time available and a briefer summary was published by Yamaguchi in the same year. The latter has formulated a useful summary of the factors which had, up to that time, been studied, and proposes a standard terminology by which those factors may be correlated. Since these already approximated to fifty and the number has since been added to, only the more important can be considered here.

A striking character of many varieties of rice is the colour, due to an anthocyanic pigment, which occurs in many of the plant tissues. These coloured varieties offer a wide range of variation both in the intensity of the pigment and in the organs in which it occurs. Though the inheritance of colour has been studied by many since the original investigations of Hector and Parnell, no complete solution has yet been worked out. In these varieties

certain defined patterns, such as leaf-sheath, apiculus and stigma all coloured, appear to be inherited as a whole, but the evidence indicates that this results from a close linkage rather than from a single factor. There appear to be two complementary factors for pigmentation to which may be added a number of localization factors controlling the organs in which the colour will appear. Hector (1922) has given a list of the groupings found in the Indian forms, while Jones (1930) has supplied a similar list for a number of Japanese forms. The latter adopts a tri-factorial basis to interpret the results obtained by him, but notes the need for further investigation for the establishment of full concordance between the results of different observers.

In certain rices the hulled grain shows pigmentation and the colour is developed in the pericarp which the process of milling is designed to remove. Owing, however, to the irregularities of the surface of the grain, the removal is rarely complete and the character has a certain economic importance. Pigmentation here ranges from purple, through red and grey-brown, to white, a range of colours which Parnell (1922) attributes to the interaction of at least four factors.

A further character of the grain gives to certain rices the title of glutinous. The title carries a false assumption, for these rices do not contain gluten; a better term would be dextrinous. The characteristic feature of such rices is that, on boiling, the grain breaks down into a sticky paste. Actually the difference rests in the presence of a soluble starch, dextrin and maltose, in place of the ordinary starch found in the common rices. Being a character of the endosperm, it illustrates the phenomenon of xenia, a fact which was first demonstrated by Hoshino (1902), and Parnell (1921) has shown that the pollen bearing the glutinous character can be differentiated from pollen bearing the starchy character by microchemical tests. The dominance of starchy endosperm was first demonstrated by Moquette (1905) and later by van der Stok (1910). These results have been confirmed by several later observers though Yamaguchi (1918) has shown by the iodine test that dominance is incomplete. In numerous instances, however, there occurs a definite departure from the expected ratio

of three starchy, to one glutinous, grains, the excess sometimes being of starchy and sometimes of glutinous, grains. Such a departure from theoretical numbers was observed by Parnell, who found, by microchemical tests, that the cause did not lie in a differential rate of production of the two classes of pollen grains and called in a differential germination to explain the facts. Chao (1928), who has also found a deficiency of the recessive form, was led to conclude a differential rate of growth of the pollen tube. More recently Enomoto (1929) has investigated the behaviour of a glutinous rice which arose in a culture of starchy rice. The offspring of this plant on selfing gave rise to heterozygous starchy forms which, in their turn, showed a deficiency of glutinous offspring. He expressed the view that the original plant arose as a recessive mutation and that in its offspring a proportion of mutations of the reverse nature, back to the dominant form, have occurred.

In many varieties of rice the lemma carries at its tip a long awn the value of which, from the economic aspect, is disputed. On the one hand, the miller prefers an awnless grain, but to the agriculturist, especially in those countries abounding in bird life, the awn possesses a certain advantage as it offers a measure of protection against depredations. The character has been studied by several observers, and the results show a far from simple inheritance. Partly, no doubt, this is due to the variable nature of the character itself; partly it is due to a varietal difference in the intensity of expression of the character, the awns being in some varieties strongly, and in others weakly developed. As Jones (1927) has pointed out, environment appears to play an important part in the determination of the manner in which the character is expressed; for certain awnless varieties sometimes develop awns on the secondary culms, and it is necessary, therefore, for this study to select parental types with care. In the cases studied by him he found evidence of both mono-, and bi-, factorial inheritance. The evidence since the early work of van der Stok (1910) indicates that the awned form is dominant and that, while many cases may be explained on the basis of one or two factors, there are others which do not offer any such simple solution.

Chao (1928) finds two factors one of which develops a more intense expression of the character than the other.

A character which is of considerable economic importance is that which Ramiah (1930) terms habit. This habit may be compact, when the culms are erect, or spreading when the culms lie at an angle with the vertical. The morphological basis lies in the tillers which, in the latter case, are procumbent and thus exhibit a character common in the wild rices. From a study of natural, as well as purposive crosses, he deduced a monofactorial difference with dominance of the spreading habit. He notes, however, that the intensity to which the spreading habit is developed varied much, and defied attempts to establish class limits, a fact which, when considered in the light of the existence of varieties exhibiting the spreading habit in different degrees, suggests that the phenomenon is not to be so simply interpreted.

Several other morphological characters have been subjected to investigation, notably those that might be expected to bear a relation to yield. Of such a nature are panicle length, spikelet stem length, culm thickness, tillering capacity and leaf measurements. These are quantitative measurements and as such would be influenced by heterosis with consequent complication of the results. Heterosis is not prominently displayed by rice, but Jones (1926) has demonstrated its occurrence in the increased number of culms per plant, a character likely to affect yield.

In addition to the variations in culm length which characterize the various races of rice, definitely dwarfed plants are occasionally found in the rice fields and cultures. Such a case was investigated by Parnell (1922), who found it to be a recessive form giving, when crossed with the parent type, a simple 3 : 1 ratio. Such dwarf forms appear to arise as mutations and have been studied by Sugimoto (1923) in Japan where their appearance in the fields is frequent. In his cultures the dwarf plant behaved as a simple recessive, with one exception, when it behaved as a simple dominant; there appear, therefore, to be two distinct races of dwarfs.

The last morphological character to which reference need be made is that known as shattering. The firmness with which the

ripe grain is attached to the rachis varies widely in different varieties, and in extreme cases a light wind is sufficient to cause the grain to fall. It is obviously an important economic character, especially in those few countries, like California, where rice is grown over large areas and harvested by machinery. It is a character which is shared, as Graham (1927) has shown, with wild rices and appears to be associated with the capacity to lie dormant from harvest till the onset of the next rainy season. Takenouchi (1924) has shown that the morphological basis of shattering is the formation of an abscission layer similar to that responsible for leaf fall, and Ikeno (1927) quotes Kato as showing, in the cross between a variety with grain firmly attached and one which shatters readily, that a single factor is concerned with dominance of firm attachment.

In view of the conditions under which rice is grown, the length of the vegetative period, variously measured as the time interval from seeding to the appearance of the first spikelet or by the date of appearance of the first spikelet, is a matter of particular importance from the economic aspect. It is of added importance in view of the high physiological specialization of the rice plant. Here again, however, very divergent results have been obtained by different observers. Hoshino (1915) found from a cross between an early (83·8 days) and a late (113·2 days) variety, an F_1 which headed out in ninety-four days, that is, the F_1 plant was intermediate with an approach to the early parent. The results obtained in the later generations indicated a tri-factorial basis. van der Stok (1910) found an almost complete dominance of earliness, but obtained in the F_2 a series exhibiting a wide range of variation transgressing both parental limits. Jones (1928) found transgression beyond the parental limits to occur sometimes even in the F_1, while the extreme F_2 plants of his cultures bred true. Here, again, the wide range of varieties which has entered into the experimental work is a contributory cause of the discordance in the results, concordance between which will only result from more extensive investigations. The problem is complicated by the apparently strong photoperiodic reaction to which rice responds.

The rice plant is not immune to functional disorganizations of various sorts, and, in certain cases, the pathological condition has been definitely traced to the action of heritable deleterious factors. Two classes of such a pathological condition have been investigated. The rice plant, like so many cultivated plants, exhibits the phenomenon to which the somewhat loose term, chlorophyll deficiency, is given. This phenomenon is not, in all cases, identical. Takezaki (1923) and Kondo and his associates (1925) have investigated cases in which the deficiency is localized and gives to the plant the typical streaked appearance known as variegated. By crossing a streaked with a normal plant, this form of deficiency was shown to be inherited only through the mother plant and it corresponds, therefore, to the similar phenomenon studied by Correns in *Mirabilis* and by Gregory in *Primula*. Deficiency of a different form has been described by Ramiah (1930). He notes the appearance of pure white seedlings as a common feature of the cultures at Coimbatore. As such seedlings died as soon as the reserve material of the grain was exhausted, the character could only be studied in the heterozygous form. He found the normal green colour to be dominant, and since he obtained ratios of 3 : 1 and 15 : 1 as well as others more complicated, there appear to be several factors concerned. A further, and independent, case of deficiency is also noted by Ramiah. In this case the seedling is yellow in place of white, the plant is slow of growth, but attains maturity and the appearance gradually changes until, in the older plants, it is difficult to distinguish from normal plants those derived from yellow seedlings. The yellow condition is here dominant and Ramiah concludes from his observations that two independent factors, both capable of producing the full effect, are responsible. Ramiah further indicates the possibility of a lethal factor occurring in a cross between a plant with purple glumes and purple pericarp and a plant with green glumes. All purple-glumed plants in subsequent generations exhibited a lighter shade of pigmentation than that of the parent, and this was associated with a 2 : 1 ratio. He interprets the result as due to a lethal factor preventing the formation of the pure homozygous dominant form, adducing as confirmatory evidence

the existence of a large percentage of unset chaffy grains on the panicles of the purple-glumed plants. It is noteworthy that these results were obtained in the offspring of the only plant of the culture with purple glumes and white pericarp, the only plant, that is, in which the closely linked characters of purple glume and purple pericarp had parted company.

The second class is characterized by a certain defective capacity to set seed. Sterility is, of necessity, a difficult subject to study, for it is not easy to differentiate between an inherent lack of capacity to set seed and a simple failure in pollination. It may be due to a purely fortuitous effect of the environment, an aspect which has been investigated by Fukuchi (1931) and Iwatsuchi (1931) the latter of whom shows that, while there is an 11 per cent. difference between good and bad yield, there is only a 2 per cent. difference in grain weight and it is, therefore, a difference in the number of grains which controls yield. On the other hand, it may be due to the action of a specific organism. In rice the *eel-worm* (*Tylenchus*) is capable of rendering whole tracts barren. Nevertheless, several cases of inherent sterility have been demonstrated in rice. That due to sexual incompatibility when rices of divergent strains are crossed has already been noticed, but other examples of complete sterility are not unknown. Sugimoto (1923) has studied eight sterile plants which arose in a single family of a pedigree culture. In these pollen did not develop and the gynæcium lacked a stigma. By investigating the offspring of the normal plants in the family he found a monofactorial difference with the sterile form recessive. The original sterile plants must, therefore, have arisen through the prior mutation of a single dominant allelomorph in the homozygous parent. Nagai (1927) has investigated three further cases of complete sterility in which the functional cause was respectively, abnormality of stamens, of gynæcium and of both organs. In each case the sterile form is recessive and three factors are concerned, two of which are completely linked, while the third is independent.

Of more common occurrence than complete sterility are cases of semi-sterility in which a varying proportion of the flowers of

the panicle fail to set fruit. Though individual cases of such sterility may be the result of fortuitous failure of pollination, certain races were early recognized, as the investigations of van der Stok have shown, to owe the character to heritable causes. The percentage of sterile flowers varies much in different races attaining, in some cases, to over 50 per cent., and environmental influence is shown by the manner in which this percentage varies in a single race from season to season. Further, in van der Stok's observations, the sterile flowers are not distributed equally throughout the panicle, the number being least in the earlier maturing portions of the panicle. In crossing two semi-sterile strains showing different intensities of sterility, van der Stok obtained transgression of the parental limits in both directions. Kondo and Ono (1923) obtained from a pure culture of *Sinriki* rice a single semi-sterile plant which bred true. It differed from those obtained by van der Stok in that the sterile flowers were evenly distributed throughout the panicle. More complicated cases have been described by Terao in a series of papers (1917, 1921 and 1922). In certain of these the semi-sterile form is a mono-factorial recessive but yields a deficiency of semi-steriles. Further, the semi-sterile plants yield a mixture of semi-sterile and normal plants, a result which may be interpreted as a reverse somatic mutation. In another case, the proportion of normal plants was in excess, indicating the continuance of somatic mutations from the recessive to the dominant. In yet a further case two semi-sterile plants were found in a pedigree culture of *Sekyama* rice. These, and the semi-sterile offspring derived from them, invariably yielded normal and semi-sterile plants in equal proportions, while all the normal plants bred true. He explains this case by assuming that the factor for semi-sterility is lethal to the extent that it prevents the formation of female gametes which, therefore, only carry the gene for normality. Ramiah (1931) has reviewed the evidence collected in India on the same subject. Clearly Yamaguchi is right when he states that further experiment is necessary before a conclusion on the matter of semi-sterility can be reached. Throughout this work the occurrence of mutations has been called in to explain the observed facts

of semi-sterility. It is not the only character in which mutations have been observed for Sugimoto (1923) refers to certain dwarf mutants and to others characterized by grain modifications.

The rice plant is subject to numerous diseases, perhaps the most destructive of which is the *eel-worm*, for this may render whole tracts unproductive. But a further, and important, disease is that known as *blast*. The term is an indefinite one, and the symptoms may be caused by cultural defects, but a common cause is the fungus *Piricularia oryzæ* Bri. et Cav., which is found throughout the rice-growing countries. Varieties show different degrees of resistance, though none are immune, and immunity tends to weaken, indicating a capacity for physiological adaptation on the part of the parasite. Nagai and Imamura (1931) trace a relationship between resistance and the number of stomata on the neck of the panicle, but it is a relationship which holds only for the Japanese rices, for other rices are more resistant though they possess a much greater development of stomata. The attack develops as the season advances and, in consequence, early varieties suffer less than late ones. Susaki (1922) has studied the inheritance in a cross between a resistant and a susceptible variety, and finds a mono-factorial difference with resistance dominant.

The above brief account summarizes the more important investigations on the genetical constitution of the rice plant. Throughout repeated evidence of linkage has been found and preliminary attempts have been made to draw up a chromosomal map. Yamaguchi (1926) and in a series of later papers has identified four linkage groups, while Chao (1928), in a detailed study involving twenty-five characters, has identified three definite linkage groups with, possibly, a fourth. In the first of these, Yamaguchi's second group, lie four and, possibly, five characters, while in each of the other groups lie two. Any linkage in the case of the other characters studied was not identified. Much, therefore, remains to be investigated before the independent observations can be harmonized and a clear understanding attained. The difficulties in the path of such harmonization lie in the large numbers of varieties available for study and in the

division of these into two groups showing a certain degree of sexual incompatibility which raises doubts as to whether the factors responsible for a particular character common to both groups are one and the same. On the other hand, the great varietal range offers peculiarly favourable material for practical improvement of the rice crop through the isolation of pedigree cultures.

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SORGHUM (*ANDROPOGON SORGHUM* BROT.)

The name *Sorghum* is applied to a large number of very diverse plants widely cultivated throughout the drier areas of tropical

and subtropical countries of both the old and the new world. These Sorghums have been under cultivation from prehistoric times and are not definitely known in the wild state. The wild plant to which they show the closest relationship is the very variable *Andropogon halepensis* Brot., which is grown in the United States as a fodder crop under the name of *Johnson grass*. As with it, the home of the Sorghums appears to be the tropical regions of the old world. The main difference between *A. Sorghum* and *A. halepensis* lies in the perennial habit of the latter, but the distinction is not sharply defined, and the same holds true of the jointed pedicel of the spikelet, at one time supposed to be characteristic of *A. halepensis*.

The uses to which the Sorghums are put are very diverse. As grown by the indigenous races of Africa and Asia, their main use is as food, and in the former continent, the flour prepared from the grain was the staple food for some races, as it still is of many, until it was superseded by maize. Requiring a dryer climate than maize, it still remains the staple food of the population of such countries as the Sudan where the rainfall is inadequate for the growth of maize. The grain is, too, largely used as feed for stock and in many countries the plant is extensively grown as fodder, though care must be taken when feeding it green to cattle since, under conditions not clearly defined, the leaves contain prussic acid in lethal amount. In this connection it is noteworthy that *Sorghum* crosses with *Sudan grass* (*Sorghum sudanense* Piper), a native of the Sudan and introduced into Australia as a fodder, and that the cross develops even stronger lethal qualities than the *Sorghum* parent (Moodie and Ramsay, 1929). The presence of such adventitious crosses in *Sudan grass* has rendered it suspect as a fodder crop. As dry fodder the culms are largely used in India, while in the United States the sweet *Sorghums* are grown for the production of syrup from the culms and the dry-stemmed *Broom corns* are grown for the manufacture of brushes from the immature panicles.

The difficulty which is so commonly met with in attempts to classify widely distributed plants of old standing in cultivation, is not absent in the case of *A. Sorghum*. Even the generic defini-

tion is questioned. The group covered by the term *Sorghum* forms, in fact, a series extending from the *Broom corns* at one extreme, with a dry pith, to forms with a juicy, saccharine, pith at the other. They have been grouped into the following species, or cultural groups, distinguished less by definite morphological characters than by country of origin.

Sorghum vulgare Pers., var. *technicus*. Characterized by its short rachis and dry stem. Grown chiefly in the Mediterranean region and the United States. It is commonly known as *Broom corn*.

Sorghum Caffrorum Beauv. *The Kaffir Corn* of South Africa. It merges into the sweet corns.

Sorghum caudatum Stapf. Grown in tropical central Africa. It is the *Feterita* of the Sudan.

Sorghum cernuum Host. Grown in North and West Africa.

Sorghum Durra Stapf. Occurs in many varieties. It is the *Durra* of the Sudan.

Sorghum Roxburghii Stapf. A cold-weather crop of western India where it is grown under the name of *Shallu*.

Sorghum saccharatum Koern. The *Kaoliangs* of China, the *Jowars* of India and cultivated also in Egypt and the United States.

The African forms have been recently described by Ivanov (1930).

The plant typically produces no tillers, but gives rise to a single strong culm which may attain a height of 15 feet or over, from the apex of which a single inflorescence, the panicle, arises. The panicle is much branched with internodes sometimes elongated and sometimes much condensed, giving rise to the loose and congested heads respectively. The peduncle is erect or, in the goose-necked forms, recurved. The spikelets are borne in pairs, a sessile hermaphrodite, and a sterile neuter also called male, as these sometimes bear functional stamens. At the apex of the branch the hermaphrodite spikelet is accompanied by two neuters. The fertile spikelet is enclosed by two glumes and contains a sterile and a hermaphrodite flower. This latter typically consists of a lemma, which may carry an awn, a palea, two lodicules, an

andrœcium of three stamens and a caryopsis. In many varieties a full complement of the organs is not carried by the fertile spikelet. The structure of the spikelet has been described in great detail by Cowgill (1926) and the characters it presents are used to classify the sweet Sorghums.

The flowers open in descending order, the first organ to appear between the expanding glumes being the bifid, plumose, stigma. The hour of opening of the glumes is much influenced by environmental conditions, Koernicke (1885) found the period of maximum opening to be between 8 a.m. and 9 a.m. Graham (1916), on the contrary, found this to be between midnight and 4 a.m. with only stray flowers opening in the daytime. A similar variation in the hour of opening has been noted in the rice plant between the hour of flowering in the tropics and in more northerly climates and the difference was there clearly associated with environmental conditions, particularly temperature. With the opening of the glumes the anthers are usually rapidly extruded and become pendent, the whole process occupying a variable time, but normally about ten minutes. In some varieties, especially those of the compact type, the anthers are frequently not extruded. The time of dehiscence is variable, but, in extruded anthers, the pollen is only shed when these have become pendent. The flower is, thus, protogynous, but pollination is normally effected by pollen from a flower placed higher up on the same panicle. Cross-fertilization is, however, possible, especially of the terminal flowers and it may also be effected by insects, especially bees. In the loose panicled varieties Graham found natural cross-fertilization to take place to the extent of some 6 per cent., while, in the compact varieties, he found only 0·6 per cent. Karper and Conner (1919) studied the offspring of *White Milo* plants scattered in a field of *Yellow Milo* and found an average of 6·18 per cent. cross-fertilized plants in the offspring.

Purity of crop, under the rough and ready methods of native cultivation, is never attained, and the main varieties have probably arisen through the assumption of a dominating position by the particular varietal element best suited to the particular locality. Selection, especially in America where all the more important

varieties have been introduced since 1850, has resulted in the establishment of a number of types; but the extent to which natural cross-fertilization takes place is sufficient to compel special measures if the type is to be maintained. For this purpose mass selection is adopted, but it is a negative process merely aiming at the maintenance of type rather than improvement. Line selection has been employed, but the possibilities of improvement by this means are, as Finnell (1930) states, limited. The available material on which selection may play requires to be extended by deliberate crossing.

Efforts have been made to analyse the characters responsible for yield. Martin (1928), working on the grain Sorghums, finds yield per acre more closely correlated with the number of heads per acre than with size of head. In Texas (1927) the correlation between weight of head and a number of plant characters has been determined in Kaffir corn and of these the more important are, with length of head $r = +\, 0{\cdot}70 \pm 0{\cdot}01$, with diameter of plants $r = +\, 0{\cdot}38 \pm 0{\cdot}02$, with length of seed branches $r = +\, 0{\cdot}59 \pm 0{\cdot}01$ and with weight of green fodder $r = +\, 0{\cdot}72 \pm 0{\cdot}01$. Significant partial correlation coefficients were obtained for weight of head with length of head ($r = +\, 0{\cdot}30 \pm 0{\cdot}02$) and for weight of head with weight of green fodder ($r = +\, 0{\cdot}34 \pm 0{\cdot}02$).

Any genetic study of the Sorghums is of comparatively recent date and present knowledge of the factors involved is somewhat restricted. Chromosome counts have been made in Texas (1929) of a considerable number of varieties and, with the exception of a single plant of dwarf Milo, the haploid number was found to be 10. In the exceptional case the number of chromosomes found from counts made on pollen mother cells varied from 10 to 12. The number found in the case of *Sudan grass* was, similarly, 10, but in *Johnson grass* the number found was 20. These results are confirmed by the observations of Huskins (1930), who studied twenty-four species and varieties of *Sorghum* including *Johnson grass*, and by Nakajima (1931).

The study of qualitative characters in crosses between plants belonging to different groups and varieties of *Sorghum* is much complicated by the occurrence of heterosis. As Conner and Karper

(1927) have shown, the phenomenon is very strongly developed in such crosses, but it is found to a slight extent only, or not at all, in inter-strain crosses of the same variety. The most recent evidence of the phenomenon is given by Reed (1930). Studies on the inheritance of height are rendered difficult on this account, but certain tall mutants which appeared in two strains of *Kaffir corn*, when crossed with normal plants, gave a normal ratio, indicative of mono-factorial difference, of three tall to one normal. A further study has been made in Texas of certain characters connected with the panicle in a cross between pure-bred strains of *Kaffir corn*. The length of rachis, number of nodes to the head and the number of seed branches all showed a definite 1 : 2 : 1 ratio indicative of mono-factorial differences in each case. The length of the seed branches proved more complicated and was not fully analysed.

The grain characters, being quantitative, have received the greatest attention and were first studied by Graham (1916). Working with the natural crosses on which he based his observations concerning the extent of natural cross-fertilization, he found yellow colour in the grain to be a simple dominant to white, and red colour a simple dominant to yellow, while plants impure for both characters gave 9 red : 3 yellow : 4 white, indicating that the factor producing the red colour was operative only in the presence of yellow. Sieglinger (1924) and Swanson (1928) have more recently studied grain colour in greater detail. Pigmentation is shown to occupy different tissues of the grain. Winton (1902) had shown some years previously that, in some varieties, a nucellar layer persists. In this nucellar (hyaline) layer a reddish pigment may exist, but in those varieties in which a starchy mesocarp persists, the nucellar pigment is masked. The red pigmentation is confined to the epidermal and hypodermal layers of the pericarp. The colours studied could be interpreted on a tri-factorial basis, a factor for mesocarp formation with the vestigial condition dominant, a factor for nucellar pigmentation and a factor for pericarp pigmentation. The remaining tissues of the plant are not pigmented. A full analysis of grain colour remains to be made.

The Sorghums have afforded instances of more than one type

of chlorophyll deficiency and several cases have been studied in Texas (1929). In *Kaffir corn* a case of albinism proved to be due to a simple lethal factor with the normal condition completely dominant as tested by ten characters including weight of plant at maturity and weight of head. A further case of deficiency falling short of the lethal condition but developing a pale yellow, in place of the normal, green in the tissues, proved to be a typical chimæra inherited only through the mother parent. Semi-sterility has also been met with in hybrid *Kaffir corn*, but appears to be due to the peculiar formation of the glumes which prevents the flowers from opening and renders them cleisotogamous. A further case, in which sterility up to 96 per cent. occurred, has been recorded by Vinall (1927). In this case sterility appeared to be due to a deficiency of pollen.

Reed (1930) has summed up the evidence obtained as to the inheritance of resistance to Smut (Covered Kernel Smut) to which certain varieties are remarkably resistant. The results are not concordant and appear to indicate that resistance is dominant in some cases and recessive in others. The disease is due to *Sphacelotheca Sorghi* Link., which, however, has been shown by Tisdale and his associates (1927) to exist in more than one strain.

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CHAPTER XV

RUBBER (*HEVEA BRAZILIENSIS* MUELL. ARG.)

THE article of commerce known as rubber is the product of a large number of plants of different species, themselves belonging to a number of very diverse natural orders. Of these it will be necessary to consider one only, *Hevea braziliensis* Muell. Arg., the Para rubber tree. This tree is a native of South America and belongs to the *Euphorbiaceæ*. Little more than a generation ago the limited demand for rubber was met by collection from the various species growing in the wild state, but the rapid increase in demand has led to a phenomenal development of cultivation, especially in the east. In the early days other rubber-yielding plants, especially *Castilloa elastica* Cerv., a Moraceous plant also from South America, were introduced into cultivation, but none have been able to compete with *Hevea* which dominates, to the practical exclusion of, all others. Though in 1873 six seedling trees were introduced into Calcutta, the main introduction of the Para tree into the east was effected in 1876 when 1,919 plants raised at Kew from seeds brought from Brazil by Wickham, and about 100 plants brought as seedlings by Cross, were shipped to Peradeniya, Ceylon. An account of the early history of this introduction is to be found in the Kew Bulletin (1898, p. 241). From these plants the entire industry of the east is derived.

The Para rubber tree is a denizen of the tropical rain forests of South America and belongs to a genus of which some ten species are recognized. Inaccessibility has rendered any complete study of the genus impossible and any classification is necessarily provisional. Such information as is available has been collected by Wright (1912). From the economic aspect this is of minor importance, for the economic questions are confined to the eastern industry which is the product of the trees introduced in 1876.

The product rubber is the coagulated latex obtained from the stem of the tree by tapping. The laticiferous vessels lie in the cortical tissues and are formed by the anastomosis of ordinary cortical cells. Coagulation is effected by dilute acid, usually acetic acid, and the spongy coagulum rolled into sheets which are dried to form the raw product of commerce.

The Para rubber tree is a perennial, grown on an economic basis only in those tropical hot and humid countries where conditions approximate to those of its native land. Propagation in the past has been by seed, but in recent years the practice of budding has been introduced and is rapidly extending. The inflorescence is a panicle bearing unisexual flowers. Both flowers are found in the same inflorescence, a few female and many male, the former being borne at the extremities of the stronger axes of the panicle. The two flowers are readily distinguished, the female being larger with a broadened receptacle. According to Maas (1919) the male flower opens between noon and 3 p.m. and the female from one to one and a half hours later, but the time is much influenced by temperature and humidity which also affect the time of dehiscence of the anthers. The first, as well as the last, flowers to open are male. The stigma remains receptive for at least twenty-four hours, during which interval of time the pollen retains its viability. It is noteworthy that very few of the female flowers set to form mature fruit, according to Maas some 2 to 3 per cent., a figure greater than that found by Heusser (1919). The cause of this failure to set seed is not clear, though Morris (1929a) has noted that, though insects are to be seen frequently visiting the inflorescences, such visits appear to be limited to the male flowers. In this connection it must be borne in mind that in the east *Hevea* is an exotic and the natural agent of pollination may be absent. There is, however, some further, and as yet undetermined, cause than the failure of insects to visit the female flowers. A further complexity in connection with the question of pollination arises from the variation in relative fertility found to exist between different plants. On the one hand, it finds its counterpart in the relative fertility of certain temperate fruits, notably cherries; on the other, in the tropical canes. Morris (1929a and 1929b)

summarizes the earlier work of the Dutch investigators and gives his own observations which are, in the main, confirmatory. The *Hevea* plant appears to be in most cases self-sterile, though individual trees differ in this respect. Whether this is associated with chromosomal differences is not known. Heusser (1919) alone appears to have made any determination and found the number to be N = 8. Maas (1919) and Heusser (1921a) found the average percentage of successful self-fertilizations to be 1·7 and 0·8 in two successive years with the highest figure per individual tree at 6·9. In nine out of the fifteen trees tested no successful results were obtained. Morris pollinated 154 female flowers of three clones, sometimes with male flowers of the same tree and sometimes with flowers of the same inflorescence without securing a single success. Cross-pollinations yield a definitely higher percentage of successful fertilizations; Maas obtaining 5·6 and Heusser 10·9 per cent. At one extreme occurred no successes in 239 pollinations; at the other, 83 successes in 211 pollinations, a percentage of 39·3. In this result the male parent appears to play an essential part, for widely different results were obtained when the same female, but different male, parents were used. More recently s'Jacob (1931) has carried out further investigations on the subject and records the results of over 24,000 pollinations.

Morris, in his second paper (1929b) has tabulated his later investigations. Again he obtained no successes in 195 self-pollinations though, in a later note (1930), he was more successful. His successes in cross-fertilization varied from 30·0 to 0 per cent., and in some cases he found a wide diversity between a cross and its reciprocal. Of interest also is his observation that seed formation is not a completely satisfactory measure of success, for in some cases the seed, though apparently normal, proved defective, lacking embryo or with embryo and endosperm in various stages of arrested development; a condition found in 27 per cent. of ordinary seed collected during the same season.

Since the latex forms the valuable product, the desirability of a tree will depend on its capacity to yield latex. The determination of this capacity is no easy matter and difficulties

are encountered which are both mechanical and intrinsic to the plant. On the mechanical side, yield depends in some measure on the length of the cut, but is definitely not proportional to this length. It depends, too, on the system of cutting of which many forms have been introduced at different times, while new systems are even now from time to time advocated. Each of these requires to be subjected to critical tests such as those of which numerous records are to be found in the early bulletins of the Ceylon Department of Agriculture or that more recently made by Tengwall (1931) of the Bosch system. Results will only be comparable when the system of cutting is uniform. Further cause for discrepancy lies in the system of tapping, of which there are numerous practised. Of later comparisons Bally (1928) found differences of yield up to 30 per cent. when a two-weeks' rest alternating with a month's tapping was compared with an alternate day tapping. Yield also depends on the exact location of the cut. Cramer (1930) quoting Richard, notes that the production of latex decreases with height, being at 90 cms. or over only 50 per cent. of the yield at 15 cms. There is also a personal factor and rigid control sometimes limits comparison to the results obtained by the individual tapper.

The difficulty in the determination of yield capacity which these results indicate, receive emphasis and practical demonstration from the discussion which has arisen over the question of rejuvenation. According to one method, the trees which it is proposed to replace are subjected to an intensive tapping process during the one or two, perhaps three, years prior to their removal. By this method, at least three times the normal yield per tree will be obtained (Lord, 1929). Clearly behind the question of yield capacity lie the more fundamental questions of the function of rubber in the economy of the plant and of the method of its synthesis. How little is known on these subjects may be gathered from the discussion of the former question by Sharples (1918). With regard to the latter question, Bobilioff (1925), in the course of an investigation on the *p*H concentration of latex, was led to suppose that starch is the principal compound from which Caoutchouc originates in the plant and the subject is under

investigation by Dutch workers at the present time. Later investigations have added little to this meagre knowledge of these matters. Yield capacity is necessarily a somewhat indefinite term, a relative, rather than an absolute, measure, and measurements of this capacity will only be comparable when all the mechanical details are standardized.

Even when this standardization of the mechanical details is adopted, difficulties arise from the physiological reactions of the plant. There is a certain seasonal response which may be of sufficient magnitude to lead to the suspension of tapping owing to low yield ; and in these responses Bobilioff (1920) has shown that transpiration plays an important part, while Arisz (1924), in noting the reduction of yield at the resting period, draws attention to the irregular appearance of that period. Summers (1928) adopts for comparative purposes a standardization to 160 tappings during the year based on the normal plantation system of alternate days with allowance for wet days, but comparisons so made can only be accepted with caution. Latex, again, shows a wide range of rubber content and the only satisfactory comparison is one based on dry rubber.

A preliminary question arises as to whether yield is a definite characteristic of the tree or whether it may vary from year to year. To this question the answer is very definite ; it is that yield is a capacity inherent in the tree and seasonal variations are small compared with the differences found between different plants. A high yielding tree will maintain its relative position as long as it remains healthy. Thus tree No. 2 at Henaratgoda in Ceylon (Lyne, 1910), believed to be one of the original seedlings introduced in 1876, has proved a consistently good yielder, while, on most estates, certain trees are recognized as yielding well above the average. The earlier observations on this subject have been collected by Whitby (1920). The most marked features of the ordinary plantation population are the high coefficient of variation and the marked positive skewness of the frequency curve. In Whitby's observations 9·6 per cent. of the trees were giving 28 per cent. of the total yield, while at the other extreme, 13·7 per cent. gave only 2·9 per cent. of the yield. Grantham (1927) has

made a similar analysis of a plantation population in which he showed that, over a nine-year period, among 918 trees the average annual yield varied from 2·1 lbs. to 21·7 lbs.; with an average of 5·9 lbs., the lowest 10 per cent. yielded 2·5 lbs. and the highest 10 per cent. 11·9 lbs. From latex measurements taken once a month over a period of four years from nearly four and a half million trees, he found that 0·3 per cent. of these trees gave an average estimated yield of 14 lbs., 0·7 per cent. gave 10 lbs. and 4·5 per cent. 7 lbs., the remaining 94·5 per cent. averaging about 3 lbs. Further evidence drawn from controlled experiments is given by Bryce and Gadd (1924) and Taylor (1926). The latter author quotes the coefficient of variation of yield in mixed parentage as being variously estimated at 76·19 (Whitby's figure) and 60·32, while he finds for the 161 trees examined by him, all offspring of the same high yielding tree (Henaratgoda No. 2) and ten years old at the commencement of the experiment, a coefficient of variation in four successive years of 18·2, 29·2, 33·5 and 27·5 respectively. His results show, further that the low yielding trees develop a greater increase than those with higher productivity, so that it would appear that other factors, as yet undetermined, control yield to the extent that actual yield is not invariably a measure of potential yield.

In spite of these difficulties in the path of determining yield capacity, the differences in magnitude are of an order which renders the identification of high yielders possible even in ordinary plantation practice. Large increase in productive capacity is possible by eliminating the low yielders and by their replacement by high yielders. Under these circumstances, the importance of finding some means by which yield capacity may be determined in the young plant is obvious, and numerous efforts have been made to correlate yield with some plant character which is capable of being determined in the young plant. Sanderson and Sutcliffe (1929) have summarized these results of which the more important are the following:—

Yield and girth.

Whitby (1919) . . .	+ 0·260	± 0·02
Heusser (1921) . . .	+ 0·326	± 0·067

Yield and girth—*continued.*			
LaRue (1921)	+ 0·299	± 0·019	
Bryce and Gadd (1924) . .	+ 0·582	± 0·035	
Belgrave (1925) . . .	+ 0·39	± 0·08	
Taylor (1926) year 1921 . .	+ 0·459	± 0·04	
year 1923 . .	+ 0·378	± 0·046	
year 1925 . .	+ 0·408	± 0·045	
Sanderson and Sutcliffe (1929) at 20 inches . .	+ 0·52	± 0·29	
	+ 0·52	± 0 29	
	+ 0·40	± 0·34	
Yield and number of latex vessel rows.			
Rijks (1920)	+ 0·51		latex
Bobilioff (1920) . . .	+ 0·55	± 0·051	
Heusser (1921b) 4-year trees .	+ 0·426	± 0·082	
5-year trees .	+ 0·535	± 0·071	
6-year trees .	+ 0·536	± 0·071	
Gehlsen (1921)	+ 0·585	± 0·028	latex
15-year trees .	+ 0·578	± 0·083	latex
LaRue (1921)	+ 0·513	± 0·016	
Bryce and Gadd (1924) . .	+ 0·459	± 0·042	
Taylor (1926)	+ 0·574	± 0·037	
Ashplant (1928) 4 years . .	+ 0·37		
8 years . .	+ 0·55		
Sanderson and Sutcliffe (1929) at 20 inches. . . .	+ 0·46	± 0·036	
	+ 0·37	± 0·035	
	+ 0·343	± 0·036	
Yield and untapped cortex thickness.			
LaRue (1921)	+ 0·26	± 0·19	
Taylor (1926)	+ 0·483	± 0·041	

In addition to the above van der Hoop (1931), working with seedling stock, found a correlation between yield and girth of + 0·4 to + 0·6, a figure in agreement with the above; but in clonal stock the correlation was greater, lying between + 0·7 and + 0·84.

A further character which, it has been claimed, shows a more

definite correlation with yield than any other is the diameter of the latex tube. On *à priori* grounds there is reason for supposing that this measurement would give a higher correlation than the other characters considered; in the first place because it is the second power of this measurement which will bear a direct relation to actual supply; in the second, because the larger bore offers a lower frictional resistance to flow. The mathematical details are given by Frey-Wissling (1930). The first investigations on latex tube bore were made by Bally (1924) with entirely negative results. More recently Ashplant (1928) has advanced a definite claim of a correlation of $+ 0{\cdot}76 \pm 0{\cdot}018$, or, eliminating the variable factor, latex tube rings, a correlation of $+ 0{\cdot}83 \pm 0{\cdot}014$ between yield and latex tube bore. Though he draws attention to the necessity of confining comparison to comparable tissues drawn from comparable areas, he has, unfortunately, not recorded the method by which he made his determinations of bore, an operation recognized as far from easy. His claim has been subjected to much adverse criticism, especially by the Dutch workers, Frey-Wissling (1930) and Cramer (1931). It may be noted, however, that these authors dealt with clonal material with a lower range of yield variation than that considered by Ashplant. The method is, at best, technically difficult and his conclusion must be considered as yet unproved.

The above attempts refer to physical characters of the plant. In another direction attempts have been made to determine the actual quantity of latex in unit volume of bark and to correlate this with yield. The earliest of these experiments was made by Bobilioff (1918) and later ones by de Jong (1928). The former, working on bark, found a definite relation to exist between productive capacity and quantity of latex in unit volume of bark; the latter worked on leaf petiole and obtained no correlation between yield and rubber content, a result which may be explained by the variation in size of cells of comparable tissues both from base to apex of the petiole and from the lowest to the highest leaf of the whorl.

From the practical point of view these results must be considered unsatisfactory for they offer no ready means of identifying

high yielding plants in the nursery. The explanation, it may be suggested, lies in the fact that all these methods consider yield from the static point of view. The plant is, however, an organism and the problem is a dynamic one. It is not merely a physical question involving the volume capacity of the latex system and the rate of flow on tapping ; it is also a physiological question of the rate of formation of the latex. This latter question must remain unanswered until further knowledge of the function of latex and the method of its synthesis by the plant is forthcoming.

In the early days of the eastern plantation industry, rubber was entirely propagated by seed of which, at best, the female parent alone was known. With increasing economic pressure the urge towards planting up only high yielding stock became insistent. For this purpose two methods were open : firstly the isolation of high yielding plants capable of handing on this character to their offspring, secondly, vegetative multiplication. Both methods have been pursued, but it is from the latter that the more important practical results have been obtained. In this matter of vegetative reproduction it is the Dutch workers who have shown the way with the result that, in Sumatra, no less than 58·7 per cent. of the extensions was planted with budded stock in 1929, while 37·4 per cent. was planted with an admixture of budded plants and selected seedlings and only 4 per cent. with selected seedlings alone (Cramer, 1931). The technique of budding is now well understood, and has been described by Summers (1930) at full length. Success depends on correct selection of suitable material and technical skill and, when both are present, the failures are infrequent. The main practical difficulty has lain in the fact that all high yielding plants do not hand on their yield capacity to the budded offspring. The reasons for this are not clear ; there may be here an illustration of an environmental effect or, as Rhodes notes in a personal communication, a pathological response to disease. High yield is a recognized early response to root disease caused by *Fomes lignosus* and may last for eighteen months and, for this reason, parental yield requires to be observed over a considerable period. With the precaution implicit thereto, practical experiment alone will show which plant possesses the requisite capacity of

handing on its yield capacity. The earliest experiments in budding were made by van Helten (1918) in 1910–1913 and, on the publication of his work, systematic investigations on the method were undertaken by Cramer and other Dutch workers. A few years later similar work was undertaken in Malaya, and since then a vast amount of work has been devoted to testing out high yielding plants with regard to their suitability for founding new clones. Already many clones have been proved which, when mature, are capable of yielding 1,000 lbs. dry rubber per acre per annum and about these a very extensive literature has arisen which need not be referred to here, since it has been so recently summarized by Summers (1930). In all such practical points as ability to renew bark, resistance to disease and capacity to withstand wind strain at the union, budded plants have proved in every way satisfactory, though certain vegetative characters of minor importance in a single tree assume a practical aspect in a clone planted in pure culture. Of such a nature, for instance, is the tendency to form heavy secondary branches in A.V.R.O.S. clone 36 which is, in consequence, liable to excessive damage from wind. It is such characters, which only become prominent in pure cultures, which raise those practical questions, so much to the fore at the present time, of pure or mixed planting.

Great as has been the advance in the practical application of budding in the industry, there remain several outstanding questions which await solution. The conditions under which rubber is grown vary considerably, and it can hardly be doubted that further experience will show that certain clones are better adapted to certain of these conditions than others. The question here raised is one for the future ; for the present, the improvement shown by budded trees from proved stock is so great that these individual differences sink into relative insignificance. Further, inasmuch as soil plays an effective *rôle* in controlling growth and it is the stock which maintains contact with the soil, this question involves the suitability not merely of the scion, but of the stock. Definite information on this matter is lacking, and provided the seedling stock is selected for vigour of growth and uniformity, favourable results will be realized.

While budding has become the main centre of practical interest, inasmuch as it offers the readiest means of multiplying high yielding stock, the possibility of establishing high yielding strains capable of handing their yield capacity to their offspring through the seed has not been overlooked. In view of the complexity shown by the process of fertilization described above, the problem is no easy one. The dominant position assumed by self-sterility precludes the straightforward extraction of a pure strain by inbreeding, and under these circumstances a minimum of two strains, each pure with regard to the factors controlling yield, will be required if a reasonable prospect of practical success is to be obtained. In the absence of any knowledge of these factors except that they are almost certainly numerous, it cannot be assumed that the two strains, even when both are pure when judged by the behaviour of their respective offspring, will give, when crossed, offspring of uniform high yield. And, in addition, there is the further complication that the two strains may be mutually sterile. Under these circumstances progress is necessarily slow. The earliest attempts to propagate from seed of high yielding trees were limited to the collection and sowing of seed from high yielding plants. Of this " illegitimate " seed, to use an expression drawn from the Dutch writers indicating seed derived from open pollinated flowers, it must be remembered that one parent only is definitely known. In Ceylon, Henaratgoda No. 2 tree has, in this manner, provided a series of trees studied by Bryce and Gadd and Taylor, to whose work reference has already been made. At fifteen years the yield per tree varied from 13·4 to 3·1 lbs. dry rubber with an average of 7·2 lbs. per tree, or 648 lbs. per acre, a yield much in advance of that obtained from the use of average plantation seed, but much below that obtainable from budding. Similar results have been obtained by Dutch workers in Java whose work has been reviewed by de Vries and his colleagues (1929), and in Sumatra where a far-reaching series of investigations has been conducted by Heusser. In the latter case, the worst of the selected mother trees, as judged by its own yield, proved to be the best when judged by the average yield of its offspring, while the best of these offspring yielded nearly seven times as much as

the worst. Heusser (1929) has proceeded further and obtained crosses between selected mother trees as early as 1920, and he has recorded the tapping results for the three seasons 1925–1926 to 1927–1928. These experiments involved twenty parent trees in thirty-five combinations and he found it possible to identify capacity to hand on high yield in certain of the parents by the relatively high yield of the F_1 families into the parentage of which they enter. In the case of some of the individual trees the yields are amazingly high considering the age of the trees. He notes, however, a tendency for the high yielders to be most susceptible to brown bast, a phenomenon generally recognized in plantation trees and explained by the physiological nature of the disease (Rhodes, 1930). He also notes that fertility is apparently a heritable character since the F_1 offspring are markedly fertile when derived from a fertile parent and, conversely, markedly sterile when derived from a sterile parent.

These results have been carried a stage further by the publication of the figures for the fourth tapping year (Heusser, 1930). These results, while generally confirming his previous conclusions, bring out certain fresh points of interest. The differences between families has become more pronounced; the family 157 × 164 maintained its lead with an average yield per tree of 7·26 kg. (15·97 lbs.), while for family 49 × 26 the average is only 3·43 kg. (7·55 lbs.). The combined yield of all crossings amounted to 681 kg. per hect. against 759 kg. for the best family and 385 kg. for the control trees of mixed parentage. The highest individual tree gave no less than 18·24 kg. (40·13 lbs.), and it is noteworthy that while there is retained in the order of trees, when ranged according to their yield in the fourth tapping, a general similarity to the order when ranged according to the sum of the three previous years, there occur marked exceptions. Thus the trees placed first, second and third in the earlier order become respectively second, third and first, the fourth drops to thirteenth, the ninth becomes fourth and the thirty-third, fifth. This tendency towards an intense increase of yield which appears in certain cases, seems to be associated with certain families and is supposed by Heusser to be an inherent character. From the practical

aspect its existence complicates the determination of the inherently high yielding tree, for continuous tapping will alone indicate its existence. He notes also the absence of any information to indicate whether high yield will be maintained or whether, as may be the case, a period of low yield will supervene.

In the same paper he deals with the results obtained from the isolated seed gardens. These gardens consist of an intermixture of two (or more) clones isolated from the general plantations and, in the case of seed produced from these, the pollen parent will be one or other of these two clones. In one case the seed will result from self-fertilization, but, in the other, cross-fertilization with the second clone will have occurred and, in the case of any particular tree derived from the seed the actual male parent will not be known. In one case, that of clones 33 and 53 interplanted, the flowering periods did not overlap, while in another, clone 36 was planted in pure culture and in both these cases the seed is considered to be the result of self-fertilization. The earliest seed, obtained in 1922, was planted and the records include figures for the third tapping of these trees. Each of the families shows a wide range of yield and some of the trees show yields much above the average, but the experiment is in too early a stage to admit any definite conclusions to be drawn. Heusser's work must rank as one of the major achievements in connection with the rubber industry inasmuch as it indicates that, though slow in yielding results, the ultimate establishment of high yielding strains capable of yielding offspring, either by self-fertilization or by crossing *inter se*, lies within the bounds of practical politics. It offers, too, as a more immediate goal, the production of " super " trees which may form the starting point of new clones.

It will have been noted that practically the entire early industry has arisen from the first importation of plants derived from the seed collected by Wickham ; and it has been questioned whether he succeeded, in such a vast country and with so small an amount of information relative to the real source of rubber, in securing the most valuable type of plant. In this matter the evidence would indicate that he was lucky. In addition to a number of minor importations into Java, an account of which is given by

de Vries, Schweizer and Ostendorf (1929b) seed was obtained by Cramer (1914) in the course of his visit to Brazil in 1913. Though he extended the knowledge relative to the variation occurring in *Hevea* in its original habitat and found a wide range of yield and even barren trees, he failed to secure any superior material from the introductions made by him.

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CHAPTER XVI

FIBRES

COTTON (*GOSSYPIUM spp.*)

THE cotton fibre which forms the raw material of the most important textile industry of the world, is a unicellular structure arising by the outgrowth and elongation of a single epidermal cell of the testa of the cotton seed. Originally the cell is a thin-walled structure, attached only at its proximal end to the testa from which it arises; it grows rapidly to its maximum length when the walls undergo thickening. In the process of ripening the walls collapse and the ripe fibre constitutes a more or less flattened, spirally twisted, ribbon. The value of the fibre depends in large measure on this natural twist which causes the individual fibres to grip when spun into yarn. Other characters, such as length, fineness and strength are of considerable importance. The whole cotton industry has been built up, and is still largely conducted, on an empirical valuation of the cotton offered, based on samples, but much labour has been spent in recent years on the analysis of the fundamental characters on which quality depends. Some idea of the complexity of this subject will be gathered from a perusal of Studies of Quality in Cotton (Balls, 1928). A further complexity is introduced by the diversity of the products manufactured from cotton, a diversity which divides the industry into sections each requiring a different quality in the raw material. The cotton grower is thus faced with an initial difficulty inasmuch as he has no very clear idea as to what constitutes the ideal quality at the production of which he should aim; and it is a difficulty felt with even greater force by the cotton breeder. In broad outline this is usually settled for him, for the major divisions of cotton quality are associated with definite types of plant, each of which is adapted to a certain, somewhat restricted, environment. Within those

limits, which it is not impossible that breeding may overcome, there is a sufficiently wide range to render the question of quality a baffling one.

Though the bulk of the world's cotton crop is raised as an annual growth, the plant is, in all cases, a facultative perennial and may be grown as such where seasonal drought and cold are insufficient to cause death. From the seed arises an axis of indefinite growth bearing leaves in the axils of each of which is a main and an accessory, bud, the position of the latter being definite, either to the right or left of the main bud. The habit of the plant is, in the first instance, determined by the behaviour of the main axillary bud. Those of the lowest leaves usually remain dormant; from the more distal buds branches arise which may develop either into monopodia, thus repeating the form of the axial stem, or into sympodia, in which case each node will terminate in a flower with growth carried on by the axillary bud (Leake, 1909). While the development of monopodial secondary branches is rarely suppressed entirely, it is invariably the case that the change from the monopodial to the sympodial type of branch is abrupt. Further, the point at which the change takes place is of varietal significance. At one extreme is the monopodial type, with only a few sympodial branches developed late at the apex of the main stem; at the other, the sympodial type with few or, in the case of individual plants, no monopodial secondary branches. The former are late flowering types, the first flowers being produced only after some 150 days, either at the apex or on tertiary sympodia arising from the main axillary buds of the monopodial secondaries. The latter are early flowering, the first flowers being produced low down after some thirty-five to forty days, on the lowest sympodial secondaries. The branching habit is of considerable importance in countries where climatic conditions, as in the case of so many cotton-growing areas, impose a definite limit to the growing season.

A further point arising out of this habit, and having economic significance, lies in the fact that the inflorescence is diffuse. When once sympodia commence to form, flowers will arise and growth and flower formation become almost synonymous terms. The

harvest is thus of indefinite duration. It commences as soon as the bolls arising from the first flowers mature and continues as long as the plant grows. This habit of indefinite fructification which has been investigated by many and most recently by McClelland (1931), adds materially to the difficulties of the cotton grower. On one hand he is concerned with quality, but quality as a character inherent in a particular plant is, largely owing to this habit, hardly definable. Cotton, in a way that has hitherto baffled analysis, is sensitive to environment. Dealing with the Indian forms of *G. herbaceum*, Venkatraman (1930) finds a progressive decline in, among other characters, lint weight in successive bolls of the same sympodium and in bolls of secondary sympodia in comparison with bolls of primary sympodia of the same age. Balls (1912) has shown that the cotton fibre grows in length up to some thirty days before the boll matures, after which thickening takes place, and reaches maximum thickness some eight days before maturity. Consequently between length and thickness no correlation exists for the one is correlated with the environmental conditions prevailing some three weeks earlier than the conditions influencing the other and between these sets of conditions no correlation exists. Quality will, thus, vary from season to season and even from boll to synchronous boll (Ayyar and Rao, 1930). Other differences which are reflected in quality occur as between different fibres within the same boll according to their position on the seed and according to the position of the seed in the locule; the failure of seeds to develop will cause "motes" to appear in the cotton or failure of individual fibres to thicken will cause "neps."

The grower is concerned, on the other hand, with the equally important aspect of the crop, yield. Yield, the weight of lint produced per acre, is a complex character and has been analysed by Harland (1929d) into the following components (see p. 297).

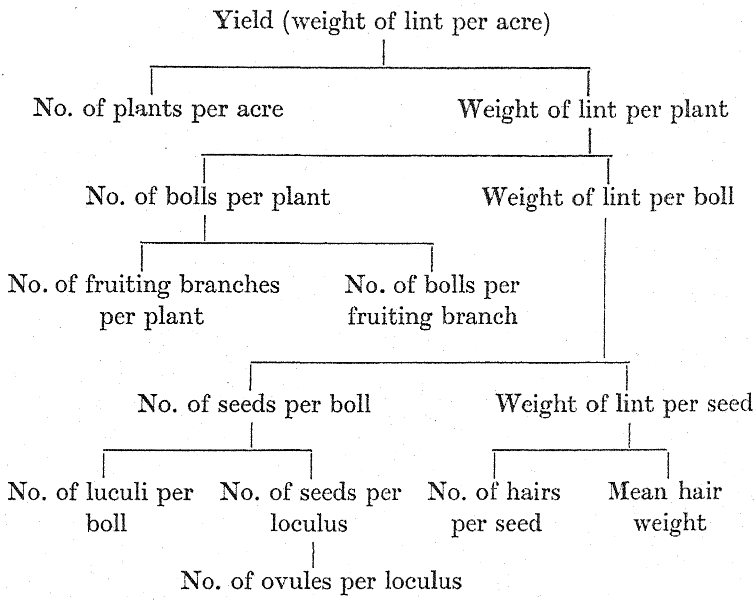
It must, however, be noted that yield, of itself, is not a simple measure of desirability for, under the conditions described, the practical aim is to obtain that balance between yield of varying quality which will give the maximum financial return. Here a further difficulty arises. As has been noted, owing to the con-

PLATE XIV

Gossypium arboreum L. Monopodial type.

By courtesy of The Secretary of State for India. *Reproduced from " Mem. Dept. Agric., India."*

[*To face p.* 296.



formation of the plant, once sympodia are formed growth becomes to a considerable extent synonymous with flowering. Flowering is, however, in no sense synonymous with fruit production. The sympodium inevitably forms a flower bud, or "square" at each node, but shedding of the square or of the boll derived therefrom is a feature with which all who have practical experience of cotton growing, are only too familiar. In part it is a heritable character inasmuch as some types of cotton will shed more freely than others under a given set of conditions, but it is fundamentally a physiological reaction to climatic environment. The question of shedding is not fully understood. Mason's investigations into the subject in St. Vincent (1922) support the general conclusion of Balls (1912) that the physiological cause is a dislocation of the water balance of the plant.

Perhaps the clearest conception of yield may be gained from the consideration of the plant as a factory in which the elaboration of a certain amount of food takes place daily, though the phenomenon

is undoubtedly a complex one, and, as Imamdar, Singh and Pande (1925) have shown, not as simple as the following exposition might appear to indicate. That food may be consumed in vegetative or in reproductive vigour. Vegetative vigour, from the habit of the plant, entails flower formation, and as more and more bolls set, the reproductive demand will come to predominate ; vegetative growth and, consequently, flower formation, will diminish and may even cease. As Mason expresses it, " both the cessation of growth in the main axis and the augmented susceptibility to shedding were attributed to a correlation factor which tended to deflect the supply of elaborated food from the apical part of the plant to the fruit developing on the basal fruiting branches." As the bolls ripen, food supplies will be liberated for fresh vegetative growth which will again be checked by fruit formation. As in the coconut, assimilative capacity appears as a limiting factor. Periodicity in flower and fruit formation is, thus, a normal habit of the cotton plant if it be correct to apply the term, normal, to what is perhaps a somewhat rare occurrence. This rarity is, however, the consequence of shedding produce by environmental causes as noted above. If, from any such cause, the buds or young bolls are shed, food will not be diverted and vegetative growth will be continuous. An understanding of the causes which lead to shedding becomes, thus, a matter of supreme practical importance and forms a major subject of study of the Physiological Section of the Empire Cotton Growing Station in Trinidad. That one of the major factors is humidity as determined by rainfall is certain since it has been found possible to correlate yield with rainfall with a considerable degree of certainty (Leake, 1928), but the exact method by which it is brought about is doubtful. A very detailed investigation of the effect of environment on yield in the Punjab has been given by Trought (1931), who traces failure of crop in large measure to a succession of adverse influences, mainly affecting root development, which do not permit the plant to recover. From the practical aspect it will be noticed that a given yield may be arrived at in more than one way, but since quality is subject to seasonal influences, these equal yields may be of very different quality even from the same strain.

Eaton (1931) has tested the possibility of forcing yield by early defloration of the plant. He succeeded in securing increased yield with *Akala* cotton, but the application of the method would necessarily require to be tested out for each variety.

Reference must be made to yet another source of complication. Though the seed possesses a commercial value as a source of oil and cake, it is the lint which is the primary product. To secure that lint the seed-cotton harvested by the grower must be subjected to the process of ginning which separates the lint from the seed. The quantity of lint obtained from a given quantity of seed-cotton becomes a factor of considerable importance. The measure of this relation is the ginning percentage, or the weight of lint obtained from 100 units of seed-cotton. An associated, but somewhat different, measure is the weight of lint (in grammes) obtained from 100 seeds. Ginning percentage ranges in commercial varieties from 40 to 25, while a complete range down to 0, from lintless seeds, may be found within the various species of *Gossypium*. A high ginning percentage is clearly a desirable character, and where markets are primitive and the grower parts with his cotton as seed-cotton, may become the dominating factor in price fixation. The factors influencing the ginning percentage were investigated by Leake (1914) and works on the reasons for the fluctuations which are found to occur in the ginning percentage, have been reviewed by Harland (1929c).

The genus *Gossypium* belongs to the natural order *Malvaceæ* and the cotton flower is typically malvaceous. An epicalyx subtends the flower proper and is composed of three bracts which, being normally triangular, give to the flower bud the name of "square." The petals are large, convolute and showy, being white, yellow or red, with, or without, a deep red spot (or eye) on the claw. The stamens are indefinite with monothecous anthers and the filaments are fused to form a tube surrounding the pistil. The ovary is commonly tri- or quadri-locular, but the number of locules varies from two to five and may vary on the same plant. It terminates in a lobed style bearing stigmatic surfaces in number corresponding to the number of locules. The style may be exserted from the staminal tube, exposing the whole of the stigmatic

surfaces, or it may remain within the tube, exposing only the extreme tip. The flowers open shortly after dawn and within a short period the pollen is shed. By this time the stigma is receptive. The flower is ephemeral, withering by evening. The growth of the pollen tube is rapid and fertilization takes place some thirty hours after pollination. The viability of the pollen had been studied by Kearney (1923) who found that only 3 to 4 per cent. remained alive by 6 p.m. unless taken from protected flowers. The flower is normally self-pollinated, but a considerable amount of vicinism occurs through insect agency. The practical importance of vicinism has rendered it a subject of repeated study.

Vicinism was investigated by Leake (1912) in India and by Kearney (1923) in America and the whole subject has been reviewed by Trought (1930) and Harland (1930). Growing a group of red-leaved plants in a field of normal green-leaved *sakel* cotton, the former found the percentage of hybrids gradually to diminish from 0·87 at 2 metres to 0·10 at 22 metres distance. These figures, however, give no indication of the actual amount of vicinism taking place in the field. Brown (1927), who has summarized the experiments of numerous workers, among many other experiments, grew four green-leaved plants in a field of red-leaved cotton and found numbers up to 66 per cent. of hybrids among the offspring. There is in these and other observations ample evidence of a sufficient amount of natural cross-fertilization to necessitate precautionary measures if a crop is to be kept pure. Lack of such measures is responsible for the dying out of varieties which was formerly accepted as inevitable. Measures essential for the maintenance of purity in the commercial crop cannot be limited to the early stages of distribution when a variety is new and only small areas are being grown. The maintenance of purity requires a highly organized seed supply on some such system as that termed by Trought " Leake's wave system," and such an organization is of particular importance where more than one variety is grown in one tract. Care must also be taken to check that common source of seed contamination, the gin. One of the most successful organizations of this nature was that organized by Jefferys for *Sakel* on the State Domains in Egypt whereby the quality of the

Domains crop was maintained at a very high degree of purity. A complete organization for the trial of new varieties, for the multiplication of seed and for the subsequent control of the crop, has now been built up in that country (Balls, 1928). The organization of a seed supply is now recognized in all countries as a necessary accompaniment to the improvement, and even maintenance of the standard grown.

The number of varieties of cotton is innumerable; the question of their classification is a matter of considerable difficulty and even the generic limits are in doubt. In this respect cotton differs little from many other plants which have been cultivated so long and acclimatized in such diverse countries, that no clear relationship with any wild form can be established. The most detailed classification of recent times is that of Watt (1907), which does not, however, receive universal acceptance, while his addendum (1926, 1927) has been criticized by Harland (1928) on the grounds that heritable characters within freely inter-crossing groups form no sure basis for specific determination. The cultivated cottons, however, fall into two very definite groups: the old world and the new world cottons. Within these groups complete fertility is the rule; between them sterility. Until recently this inter-group sterility was supposed to be absolute, but Zaitzeff (1927) has succeeded in obtaining inter-group crosses with, however, complete sterility of the hybrid. Subsequently inter-group crosses have been obtained by Vycotski (1930) and Nakatomi (1931). In a brief note Harland (1932) records a cross between *G. barbadense* and *G. arboreum* var. *sanguinea* which developed a few viable pollen grains from which he succeeded in obtaining back crosses on to *G. barbadense.* Harland and Atteck (1931) have also succeeded in securing a cross between several species of *Gossypium* and *Thurberia thespesioides* A. Gray, the wild cotton of Arizona having 13 chromosomes. Thus they raise the question of the generic limits to which reference has already been made and the sharp distinction between the old and new world cottons is broken down. The essential difference between the two groups is chromosomal. Though a full examination of all the types has not yet been effected, Denham (1924), and later

Banerji (1929), have shown that the old world group have 13 and the new world group 26 chromosomes haploid. Zaitzeff (1928) has presented a classification based on cytological and genetic evidence in which he divides the genus into four groups, two of which are old and two new world. He points out that all groups show a complete parallelism in almost all characters. Harland (1931), less ambitious, recognizes a chromosomal difference as of primary importance and presents a classification which embraces those forms of which sufficient knowledge has been obtained and leaves the remaining forms to be fitted in as information accumulates concerning them. He recognizes that this information will also lead to a satisfactory delimitation of the genus. His classification is as follows :—[1]

Section I. 26 chromosomes.

A. Cultivated New World.

(1) *G. hirsutum* Linn. The Upland type. It includes all cultivated Uplands, with no true wild types.

(2) *G. purpurascens* Poir. The Bourbon type. It includes part of the cultivated tree cottons of the Antilles, the *Moco* cotton of Brazil and a number of wild forms ranging from Florida through the Antilles to South America. It has been introduced into Africa where it is found in the Gambia and as far south as Southern Rhodesia.

(3) *G. barbadense* Linn. The Peruvian type. It includes the cultivated Sea Island and Egyptian cottons in the sympodial group and part of the cultivated tree cottons of the Antilles, Brazil, Peru and Ecuador in the monopodial group. It comprises the *Ishan* cotton of Nigeria, the *Tanguis* cotton of Peru and the semi-wild and cultivated forms of *Kidney* cotton.

Of these, Upland and Bourbon are closely related genetically, and there are a certain number of connecting forms. They intercross with no recognizable sterility either in the F_1 or subsequent generations. The Peruvian group, while inter-crossing readily with both Upland and Bourbon, produces sterile and abnormal forms in the F_2 and subsequent generations.

[1] I am indebted to Dr. Harland for permission to quote from his unpublished work.

PLATE XV

Gossypium arboreum L. Sympodial type.

By courtesy of The Secretary of State for India. *Reproduced from " Mem. Dept. Agric., India."*

[*To face p.* 302.

B. Wild Polynesian.

(4) *G. tomentosum* Nutt. (Hawaiian Islands.) A monopodial type with the whole plant covered with a thick tomentum and small seeds covered with a thick brown fuzz and short brown lint hairs.

(5) *G. taitense* Parl. (Fiji Islands, etc.) A monopodial type differing from *G. purpurascens* in minor characters only and classified separately on ecological grounds.

Section II. 13 chromosomes.

A. Cultivated Old World.

(1) *G. arboreum* Linn. Distributed throughout India, Malaya, Burma and south China, and spreading westwards through Abyssinia and the Sudan.

(2) *G. herbaceum* Linn. Distributed through most of India, but typical of north-west India, Turkey, Persia, Iraq, Turkestan and south-eastern Europe. In Africa it spreads south to the Transvaal low veldt and Southern Rhodesia and west to the Gambia.

The classification follows that of Zaitzeff in reducing the cultivated Asiatic cottons to two species, an Indo-Chinese species grouped under *G. arboreum* and a Levantine species under *G. herbaceum*.

B. Wild Old World.

(3) *G. Stocksii* M. Mast. A monopodial type forming a low, spreading bush. It is found wild in Sind and Arabia.

C. Wild New World.

(4) *G. Davidsoni* Kell. A monopodial type found wild in lower California.

(5) *G. lanceœforme* Miers (= *Thurberia thespesioides* A. Gray). A monopodial arborescent shrub found wild in Arizona and known as Arizona wild cotton.

D. Wild Australian.

(6) *G. Sturtii* F. v. M. It is a lintless, monopodial cotton found only in desert districts of tropical Australia.

Several well-known types recognized in earlier classifications as possessing specific rank are omitted from this classification. Some of these the evidence indicates to belong to the species recognized above. Thus :—

G. hirsutum includes *G. mexicanum* Tod.
G. purpurascens includes *G. punctatum* Sch. and Thon.
G. Schottii Watt.
G. barbadense includes *G. mustelinum* Miers.
G. microcarpum Tod.
G. peruvianum Cav.
G. vitifolium Lamk.
G. brasiliense Macf.
G. lapideum Tussac.

Harland excludes from the genus the type known as *G. Kirkii* M. Mast. on the grounds that it will not inter-graft or hybridize with any known species of cotton and that it has square stems, a character not found in the genus. Its chromosome number is as yet unknown. Evidence is lacking concerning other types hitherto placed within the genus to justify any pronouncement on their affinity.

Of the cultivated cottons, those of South America have not so far been thoroughly investigated. Cook (1926, 1928) has recently described, and given specific rank to, certain forms found in Ecuador and Colombia. Their claim to such rank, however, must remain doubtful pending the necessary cytological and genetic work. In the course of centuries of cultivation the various forms of cotton, especially those of the new world, have been freely transported round the globe and, in the process, exposed to the action of environment and vicinism and any analysis beyond that based on chromosomal and genetic investigation must necessarily be a matter of speculation.

The numerous varieties of cotton which are cultivated at the present time are for the most part the products of selection. Selection has taken various forms. In Brazil, owing to the conformation of the country, cotton is grown to a large extent in isolated tracts each of which has, by a natural process, evolved a cotton suited to the local conditions. Elsewhere selection has been a more artificial process. A grower with an observant eye has noted an aberrant plant possessing qualities in one or more respects superior to the bulk of the crop. He has collected and sown separately the seed of that plant and gradually built up a

supply sufficient to introduce into general cultivation. That is the history of many of the older varieties in America, an account of which is given by Brown (1927), and in Egypt. Originally the process was simple and depended on a certain isolation and roguing in the early stages for the preservation of the improvement. In more recent years a greater certainty has been introduced by the adoption of self-fertilization which is readily accomplished by covering the buds, or merely tying these, so that the petals cannot expand. The history of *Maarad* cotton, the latest variety of importance to be cultivated in Egypt, is instructive owing to the fact that it can be traced back with a considerable degree of assurance and has been placed on record by Sennitt (1929). *Affifi* was the standard cotton grown in Egypt at the commencement of the century. It was a chance discovery, made in 1882, in a field of the then commonly grown *Ashmouni*, itself a selection from a welter of forms arising through natural crossing between *Jumel*, the first new world cotton to be grown in Egypt, a perennial form, and one of the many introduced forms, among which was *Sea Island.* The change to *Ashmouni* was, no doubt, facilitated by the advantage presented by its early (sympodial) habit. *Affifi* seed was imported into America in 1901 where, under the changed environment, it exhibited a considerable degree of diversity. Selection, using progeny rows, led, in 1908, to the isolation of divergent types, one of which has been grown in Arizona under the name of *Yuma.* In 1910 a single divergent plant, claimed by Kearney (1914) to be a mutation, was observed in a field of *Yuma.* Critical examination through three years, again using progeny rows, failed to reveal any material variation, and the plant was introduced into cultivation in 1916 under the name of *Pima.* In 1918 *Pima* was introduced into Egypt where it was subjected to rigorous control. As the result of this detailed analysis several distinct strains were isolated, some of which were sufficiently homogeneous to justify combination and multiplication, and, as a result of further field tests under the official organization for the testing of commercial varieties, have been introduced into general cultivation under the name of *Maarad.*

The question of the origin of these aberrant plants which have

played so important a *rôle* in the history of cotton, must remain in most cases unanswered. In a plant of such complex genetic constitution the appearance of certain combinations in a homozygous condition would be a sufficiently rare occurrence to correspond to the observed facts. But the manner in which, in most cases, more than one character is simultaneously affected is suggestive of mutation. That mutations occur in cotton is undoubted; the clearest case being that noted by Hutchinson (1929) of a bud mutation from a narrow, to a broad, lobed leaf in a grafted Indian cotton. Sterile dwarfs have been observed by Burd (1924) in *Sea Island* cotton and a like occurrence of sterile dwarfs appeared in certain late generations of a cross between *G. arboreum* (red, monopodial) and *G. neglectum* (a green, sympodial form of *G. arboreum*) made by the writer (unpublished).

Selection is not, however, always so fortunate as to find purity already established and in many cases the offspring resulting from the selected parent exhibit a variety of forms, a clear indication that the aberrant plant is the result of cross-fertilization. This is particularly true when vigour has formed the main basis of selection, and the underlying phenomenon is probably heterosis. This phenomenon has not been investigated in any detail in cotton, but it has been frequently recorded. It would appear a general rule that a cross involving the *Hindi* weed cotton of Egypt yields a plant more vigorous than the standard variety and such a plant is likely, therefore, to be selected as particularly striking to the eye. Brown (1927) has recorded increased vigour as the result of crossing strains of *Express* cotton which had been inbred for three years, while Kearney (1923) has noted the same phenomenon in a cross between *Holden* cotton, an Upland form, and *Pima*, an Egyptian form. An increased tendency to shed bolls with contabescence of the anthers was noted by Leake and Ram Prasad (1912) in certain Indian cottons as the result of inbreeding, but the phenomenon was not investigated and their interpretation has been questioned by Harland (1923). It would seem probable that normally a sufficient proportion of the crop arises through self-fertilization to have resulted in the elimination of the major deleterious factors. Harrison (1931) records the

occurrence of metaxenia in the cotton plant. This term is applied to the direct effect of pollen on tissues of the mother plant and was first proposed by Swingle to explain certain phenomena observed by him in the date palm. He obtained a significant reduction of lint length when *Pima* was pollinated by *Hopi* and a significant increase when *Durango* was pollinated by *Pima*. Other characters, as boll period and lint index were also influenced. It follows that selection of seed for propagation might readily tend to the selection of hybrids.

Much attention has been devoted to unravelling the genetic constitution of the various forms of cotton, but the complexity of the problem, especially where lint characters are involved, is such that, though many of the varieties now under cultivation are the products of deliberate crossing between inbred strains, the ultimate selection of an economic plant has been largely a matter of continued selection within the wide range of offspring which the original cross, together with back-crosses, was designed to supply. The more obvious characters, those of a qualitative nature such as petal spot and so on, have frequently been studied, especially by Harland (1929a and 1929b). Such observations have an economic significance inasmuch as they facilitate the detection of rogues and, consequently, the maintenance of purity. In certain respects these results, which refer to the new world cottons, indicate a greater complexity than is found for the corresponding characters in the old world cottons which were investigated by Leake (1911). On the genetic aspect of the cotton plant Kearney (1930) has summarized the available published information, but Harland (1931) has kindly supplied a later summary which incorporates both the published results and his own unpublished observations. The following brief account has been amplified from this source.

Plant characters.

(1) *General Habit.* As has been explained earlier, two very divergent types are found in all groups and to these the terms monopodial, or late, and sympodial, or early, may be applied. There is, however, no sharp distinction between them. Leake and Ram Prasad (1914) used, to record this habit, the somewhat

unsatisfactory measure of number of days to the appearance of the first flower and obtained in crosses between the extreme types an intermediate F_1 with approximation to the early parent and an F_2 monomodal, and too complex for analysis; but showing, in some cases, transgression of the early parent and, in all cases, non-reappearance of the late parent. Harland, using his much more reliable method of node number, the node at which the change in type of secondary branch takes place, found a similar situation in the new world cottons with a virtual disappearance of the late type both in the F_2 and F_3. By back-crossing he obtained evidence of segregation. The tendency of the early type to prevail has a distinct economic advantage.

(2) *Branch Habit.* The most marked variant of the sympodium is the cluster habit in which the internodes are much reduced. Thadani (1923) claims a monofactorial difference, but Harland failed to obtain so simple an explanation.

Kearney (1930) has described a type of Egyptian cotton in which the sympodium is reduced to a single internode and it owes the character to a single factor.

(3) *Anthocyanin Colour.* Harland, basing his conclusions on the work of Leake (1911), recognizes three types of anthocyanin pigmentation, the sanguineum type with red plant body, and flower and petal spotted, the green type with green plant body, a non-red flower and petal spotted and the type with green plant body and petal unspotted. These appear to form a multi-allelomorph series. In the Asiatic forms the heterozygous red condition has the colour diluted, but a single factor only is involved.

In the new world cottons red-leaved varieties occur in Upland, Bourbon and Peruvian cottons. The red colour of Upland has been investigated by many, who agree that a single factor is concerned, though Ware (1927) has found more than one strain of red indicating the presence of modifying factors. Harland finds that the factor for red in the Peruvian and Bourbon cottons is identical, but differs from that for red in Upland and that while, as Carver (1929) has shown, in the case of the Upland the red factor is independent of the petal spot factor, in Peruvian and Bourbon it may be a member of the petal spot multi-allelomorph series.

(4) *Crinkled Dwarf.* This form occurs in Sea Island cotton and forms a simple recessive to normal (Harland, 1916). When crossed with Upland an unclassifiable series is obtained in the F_2. Crinkled leaf, which occurs in Egyptian, appears to be identical with the above.

(5) *Hairiness.* This complex character has hardly received the attention it deserves in view of the recent importance it has assumed in connection with Jassid resistance. Most of the work on this complex of characters is based on inter-specific crosses and has given an unclassifiable F_2. Harland finds in the back-cross F_1 (*G. tomentosum* × *Sea Island* or Upland) × *Sea Island* or Upland, segregation into one tomentosum type : 1 non-tomentosum but with much variation in the tomentosum class.

(6) *Leaf Shape.* In old world cottons Leake (1911) using a "leaf-factor" (total lamina length of mid-rib × length petiole to sinus ÷ maximum breadth of central lobe), showed a mono-factorial inheritance for laciniation with a marked parent offspring correlation indicating the presence of modifying factors.

The new world cottons indicate no such simplicity. The main types *Okra* and *Super-okra* in Upland, and *Cassava* in Bourbon, offer examples of simple inheritance, and it is possible that *Okra* and *Cassava* are the same; but in inter-specific crosses complex results are obtained.

Flower characters. The major characters only can be mentioned.

(1) *Petal Colour.* In the old world cottons Hutchinson (1931) describes a multi-allelomorph series of factors which also govern petal length. The position in the new world cottons is not so simple, and the yellow colour is controlled by a major gene associated with a series of minor genes which modify the expression of this colour (Harland, 1929g).

(2) *Petal Spot.* Leake and Ram Prasad (1914) found in the old world group a monofactorial explanation for eye spot, the recessive eyeless form occurring in certain Chinese cottons. In the new world cottons, again the explanation is not so simple, and Harland (1929a) has classified a multi-allelomorph series associated with modifying factors.

(3) *Pollen Colour.* Much work has been done on this complex

of characters and Harland (1929f) defines nine grades produced by a major factor producing yellow and a series of modifying factors and, in *Sea Island* an intensifier.

Seed characters.

(1) *Lint Length.* Here the difficulties which accompany determinations of quantitative characters are apparent. No simple factorial explanation has been offered. The numerous investigations on the subject indicate that long lint is dominant or nearly so and that, in the F_2, a continuous series is obtained which sometimes gives indications of more than one mode. The matter is complicated by the fact that much of the work has been done on inter-specific crosses.

(2) *Lint Index.* From its definition, weight of lint on 100 gms. seeds, this character is obviously not a simple one for it depends on the mean number of hairs per seed, the mean hair weight, the surface area of the seed and the proportion of epidermal cells which grow into hairs. Lint index is, thus, partially correlated with seed weight. In spite of this complexity, Harland found that in *Sea Island* strains could be established which bred true to a large number of different means between 30 and 60 mg.

(3) *Ginning Percentage.* Important as this character is, inasmuch as on it depends the commercial value of seed cotton, it is obviously a very complex one. Not only is it dependent on several component characters, to identify which an attempt was made by Leake (1914), but some of these components are subject to environmental influences as Balls (1912) has shown.

(4) *Seed Fuzz.* In the old world cottons the seed is either fuzzy or tufted. Hutchinson (unpublished) found clear segregation into three tufted intermediate : one fuzzy. This result is not in accord with some unpublished data obtained from a similar cross by the writer who found in the F_1 fuzz to be intermediate and, in the F_2, 1,044 fuzzy and partly fuzzy seeds, forming a practically continuous series, and 225 tufted. Though the result offers no simple interpretation, fuzz would here appear to be a partial dominant.

In the new world series the position is even more complex. Three main types of fuzz distribution are recognizable : naked,

with complete absence of fuzz and lint hairs grading down to nearly absent, a type found in all three sections of the new world cottons, tufted, with a tuft of fuzz at the apical end of the seed, again found in all three sections, and fuzzy, also found in all three sections. Intermediate stages of tufted and fuzzy are to be found. The four factors which appear to have been established for these characters are :—

N — n, naked — fuzzy (in Upland).
T — t, tufted — naked (in Peruvian).
S^m — s^m, less fuzzy — more fuzzy (in Peruvian, Kearney).
F^t — f^t, tufted — fuzzy (in Upland).

There is, in the above, evidence of some relation between fuzz and lint characters ; there is also, in the Chinese cottons and crosses with these, evidence of a relation between fuzz and plant body hairiness, for the determination of naked-seeded plants could be effected by inspection of the plant before flowering took place (observations of the writer unpublished). Details of the relationship have not, however, been worked out.

(5) *Kidney Seed.* In that Peruvian type of cotton formerly known as *G. braziliense* Macf., the seeds are joined together to form a kidney-shaped mass. A tendency for seeds to adhere to each other is also met with occasionally in the Upland and Bourbon groups. In inter-Peruvian crosses there is evidence of mono-factorial inheritance, while in Upland × Peruvian crosses the typical kidney type failed to reappear in several hundred crosses.

(6) *Seed Weight.* Balls (1912) obtained in the F_1 of an Upland × Egyptian cross and in inter-Egyptian crosses intensification of size and multimodal curves in the F_2. Harland, in Egyptian × *Sea Island* crosses almost invariably obtained a monomodal curve in F_2. As Balls has noted, there may be a correlation between boll and seed size. The seed and lint develop in a cavity restricted by the size of the boll and it is conceivable, therefore, that the seed may carry a potential capacity to develop a size which cannot materialize owing to the pressures set up by the restricted space. Such a limitation to development, it may be noted, must also apply to the lint which develops contem-

poraneously within the same cavity. Preliminary efforts by the writer to test this possibility led to negative results.

Any study of the characters affecting the lint offers exceptional difficulty, not the least of which is that of determining the inherent value of quantitative characters in a structure reduplicated so many times in a single plant. A further complication is introduced by the seasonal and environmental influences to which reference has already been made. In view of these difficulties considerable attention has been devoted to the search for correlations which would offer an indirect measure of the desired character through some more readily determined character. The most detailed investigation of this nature is that of Kearney (1923, 1926), who worked out the correlations of 38 characters, involving most of the plant organs, in the F_2 of a *Holden* × *Pima* cross. Of the 703 pairs of characters for which correlation coefficients were worked out, 93 were significant and only 1 of the 38 characters, that for fuzz, showed no correlation with any other character. Between many of these characters the correlation is due, and in some cases obviously due, to physical or physiological causes, but there remain many to which it is difficult to assign such a reason. Of the 93 significant cases 66 showed coherence, or association between characters introduced by the same parent, while 27 showed disherence, or association between characters from different parents. Of these correlations two only, those between boll length and fibre length and between boll diameter and lint index, have an economic significance. Investigations of a similar nature have been made by Dunlavy (1923) with similar negative results, and Kearney (1928) sums up the available information by the statement that the only significant correlation which appears to be neither physical nor physiological is the negative correlation between fibre length and fibre colour in the Upland × Egyptian hybrid. More recently Stroman (1930) has calculated the multiple correlation coefficients for eight characters, including yield, for a series of varieties and finds values for yield with the remainder varying from + 0·99 to + 0·96 in the different varieties.

Though these observations are disappointing inasmuch as they fail to offer any great hope that a correlation will be established

between characters affecting the economic value of the product and others more readily determined, they indicate a considerable range of correlation apparently due to genetic constitution. In view of the large number of chromosomes, linkage, of which such correlation is the visible sign, would hardly be anticipated to the extent here indicated. Moreover, it must be linkage of a low order. Harland (1929d) identifies three linkage groups. The first group involves the factors for fuzz, node number, petal spot, red plant body, a petal spot modifier and a pollen modifier; the second group, the factor for crinkled and a corolla modifier; the third, a factor for yellow pollen and a factor governing the number of boll loculi. The distances between these in the chromosomal groups has not been mapped. Prasad (1922) has drawn attention to an apparent correlation between length of stigma and lint length. His observations, however, include the range of cultivated cottons, both old and new world forms, and can hardly be interpreted as demonstrating linkage.

It has already been noted that, though cross-fertilization is a sufficiently common occurrence to endanger the permanence of a strain unless adequate precautions are adopted to maintain purity, self-fertilization is sufficiently the rule in cotton to have eliminated the major deleterious factors. A few cases have, however, been recognized of which the clearest is chlorophyll deficiency. Stroman and Mahoney (1925) have studied a defect of this nature in an Upland × Egyptian cross and find the colourless plant to be a double recessive. Harland (1929d) concludes that the evidence indicates that leaf colour is controlled by three factors, one of which is present in the Peruvian group and two in the Upland. Chlorophyll pattern, where the deficiency is localized, the former authors attribute to three factors with evidence of linkage between these. A similar form was observed by the writer in a certain strain of Indian cotton (unpublished), but details were not worked out. Plants much reduced vegetatively, with complete male sterility through failure of the anthers to open and partial female sterility, are not infrequent in fields of *Sea Island* and form another example. Sterile dwarfs, to which reference has been made as appearing in certain crossed strains of Indian cottons,

may offer a comparable phenomenon in the old world group, but their mode of origin is suggestive of mutation.

The cotton plant is, in all countries, subject to numerous diseases which, in more than one instance, have become the critical factor in economic cultivation. Bud and boll shedding, though they may have considerable economic significance, cannot be classed as diseases. In some cases a phenomenon known as facultative shedding occurs. In tree cottons, monopodial types producing sympodia from about node 30, all the earlier formed buds are shed. At a certain stage an abrupt change takes place and bolls are set freely. The cause of this phenomenon is not known ; it is clearly not pathologic, and Harland (1929b) suggests that it is a photoperiodic reaction. As commonly observed, however, shedding is a physiological reaction to environment which may become, in certain instances, definitely pathological. This aspect has, perhaps, been sufficiently considered at an earlier place ; but it is a matter of common observation that different strains show marked diversity of reaction to any particular set of environmental conditions, and Kearney and Peebles (1927) have found a coefficient of parent to offspring correlation for total shedding in the F_2 of a *Pima* × *Akala* cross of $+ 0{\cdot}715 \pm 0{\cdot}085$, indicating a genetic basis for the character. The isolation of strains possessing the capacity to hold bolls under the particular environmental conditions is one of the major problems facing all cotton countries.

Diseases which are traceable to specific organisms, both fungi and insects, offer problems of considerable interest. Cotton wilt disease, of which the causative organism is *Fusarium vasinfectum* Atk., is responsible for much loss in the United States' cotton belt where the problem of remedial measures has received much attention. Though Rosen (1928) notes that most varieties of cotton, if grown under proper conditions, are resistant to wilt and that the adoption of good farming practice materially helps the control of the disease, the principal remedy has been the isolation of resistant strains built up from plants remaining healthy in badly infected fields. Among the earliest of the numerous resistant varieties are *Dillon* and *Dixie* which were obtained in this manner.

More recently resistant strains have been raised by Lewis in Georgia. Among these may be mentioned *Dix-Afifi*, as the name implies, a cross between *Dixie* and *Afifi*, and *Lewis* 63. The cause of the resistance remains undetermined, but it is definitely a resistance which is partial only and breaks down under certain conditions. Even the most resistant forms become susceptible in the presence of nematodes, the cause of " root-knot." The small amount of evidence available seems to indicate that resistance is a dominant character.

Anthracnose, a disease of which the causal organism is *Glomerella gossypii* Edg., is another disease which is responsible for extensive damage in the United States and probably most other cotton-growing countries. To it different degrees of resistance are shown by different varieties. Edgerton (1916), however, has shown that this resistance consists of a capacity to withstand infection and that, once inoculation has been effected, the capacity to throw off the disease is no greater in resistant than in susceptible varieties.

Another disease which offers points of interest is the Cotton root-rot caused by *Phymatotrichum omnivorum* Shear. It offers a typical instance of the manner in which resistance is associated with environmental conditions in such a way that resistant capacity in the plant becomes a relative, rather than an absolute character. At the conference on the subject held in Texas (Ezekiel, 1929), it was shown that the severity of the attack was closely associated with the alkalinity of the soil. The activity of the fungus is greatly inhibited by a *pH* value of 6·0. While in no variety or individual is immunity found, a differential capacity for resistance occurred, and it has been found possible to raise relatively resistant strains of *Pima* and *Akala* cottons.

Bacterium (*Pseudomonas*) *malvacearum* E. S. F., is a disease of the cotton plant which is responsible for much damage; on the boll it gives rise to the external boll disease, on the leaf to angular leaf spot and on the stem to black arm. The disease may assume epidemic form and the controlling factors are largely climatological. The extent of the attack appears, as is so frequently the case, to be linked with the healthy growth of the plant. This aspect of the problem has been dealt with by Massey (1930) and Stoughton

(1930). There is, however, strong evidence of differential varietal resistance, and Harland (1931) notes that *Sea Island,* although suffering badly when first introduced into the West Indies, responded to selection for resistance. Of inheritance to resistance little is known except that it is complex, but resistance may well be partial and limited to a strain only when grown under certain conditions.

Of insect pests which attack cotton there are many. The *boll-worms*, of which there are forms widely distributed throughout the cotton-growing areas, are responsible for an immense amount of damage. By penetrating buds and young bolls they are a contributory cause of shedding, and by penetrating maturer bolls, they cause weakened and stained lint. The larva hibernates in the cotton seed and the insect passes through more than one life cycle during the season. Unless, therefore, some natural check be applied, the numerical increase may be such as to destroy completely the later pickings. Remedial measures are directed mainly to ensuring a close season which removes the food plant, and to fumigating the seed, which kills the hibernating larvæ, but Harland (1929e) has pointed out that distinct differences in what may be termed palatability occur between different species and varieties of cotton. He suggests that it may be possible to use the F_1 of inter-specific crosses which are sterile, as a catch crop ; since the young bolls are shed, the larvæ contained in these will perish. An attempt was made in India by the writer to make use of this differential palatability as a protection against attack by the selection of strains carrying the red body colour which are definitely less palatable.

The boll weevil, *Anthonomus grandis* Boh., which entered the United States from Mexico in 1892 and has subsequently extended the range of its ravages until it has become the most important pest in that country, is a pest which is characterized by the rapidity of its multiplication, a generation occupying some seven to twelve days only. Direct control has been found difficult, the most recent and promising attempt being to dust the fields from aeroplanes, and one of the most important steps has been the introduction of early maturing varieties which will mature their crops before the

major attack sets in. The first effect of the invasion was the practical elimination of all long staple Upland varieties which were comparatively late in maturing; but the situation has been met by the breeding out of long staple early maturing strains like *Express* and *Webber*.

The blister mite, *Eriophyses gossypii* Banks, is a pest common on cotton in the West Indies. The Upland group of cottons are all severely attacked, as are also the Peruvian group in varying degrees, while the Bourbon group is immune. The resistance which some strains show to the attack of the mite has been shown by Harland (1919) to be a simple recessive. Here, again, the source of the resistance is unknown and appears to fall within the sphere of biochemistry.

In South Africa the early attempts to develop cotton cultivation received a severe check owing to the attack of the Jassid, *Chlorita fascialis* Jacobi. This insect harbours on the leaf and causes it to wither. So severe were these attacks that it seemed probable that cotton cultivation throughout the southern portion of that continent was doomed. Five varieties were at that time in general cultivation and it was noticed by Worrall (1923) that certain plants exhibited a degree of resistance not possessed by others. In 1924 Parnell commenced to make a number of selections of single plants which exhibited the maximum degree of resistance. Of these selections one, *U4*, stood out as markedly superior to all the others. Steps were taken to multiply up a stock of this strain and in 1929–1930 practically the whole of the low veldt was planted with it. *U4* has been found adapted to a wide range of conditions, and its cultivation is rapidly extending throughout the whole range of east and east-central Africa, as far as Uganda. Throughout this extensive tract it bids fair to become the dominant variety. *U4* does not owe its dominating position merely to its capacity to resist Jassid; it is free fruiting and definitely non-shedding, and it is capable of putting on a large crop in a short time, an important point in the somewhat uncertain climate of the tract. It has, however, as unfavourable characters, a small boll and a lint of medium length and somewhat harsh. The preliminary selections which the urgency of the

situation caused to be multiplied up for bulk sowings on a commercial basis have not proved to be pure in respect of several important characters and further re-selections have been made which should show a definite improvement in lint character.

Cambodia cotton, a type introduced into South Africa from India, has proved itself to be even more resistant to Jassid than *U4*, and with a view to the production of a strain having the greater resistance of *Cambodia*, this plant is being crossed with the best strains of *U4*. The interesting story of the evolution of *U4* is given in Parnell's reports in the series of *Reports from Experiment Stations* published annually by the Empire Cotton Growing Corporation. As in the case of the other diseases already referred to, the source of resistance has not been determined. A close correlation between resistance and hairiness has been noted, but, while all glabrous plants appear to be susceptible, all hairy plants are not resistant and the ultimate cause of resistance lies deeper than this. Moerdyk (1927) sums up the evidence as indicating the injection of a toxic substance by the insect, but it is not impossible that the insect acts as a vector of a virus.

A disease to which the name *leaf-curl* has been applied has recently assumed importance in the Sudan, and it is probably the same disease as that noted by Jones and Mason (1926) in Nigeria. An account of it has been given by Kirkpatrick (1930, 1931). It is a virus disease of which the vector is the *white fly*, *Bemisia gossypiperda* n-sp. (Misra and Lamba, 1929). The pathological symptoms differ with different strains and varieties and on the whole *Sea Island* cottons are less susceptible than *Sakel*, the standard crop of the major area in the Sudan, while other Malvaceous plants, as *Hibiscus cannabinus* and *H. esculentus*, may carry the infection. Certain strains of *Sea Island* showing a marked degree of resistance have been isolated and are being used in an endeavour to raise a resistant *Sakel* × *Sea Island* strain. With regard to the nature of the resistance, Bailey (1930) gives reason for supposing that resistance is associated with the development of a strong root system and that the development of the disease, as distinct from resistance to infection, depends in some way on soil conditions. The strong rooting habit of the

Sea Island plant enables it to make use of the Gezira soil in a manner which is not possible for *Sakel*. He further notes that at Shambat near Khartoum, these same strains which, in 1928–1929, had proved susceptible, in 1929–1930 were as resistant as in the Gezira; he suggests an association between this phenomenon and the presence of a hard pan below the surface. In the former year the plants came away slowly and the roots did not penetrate the hard pan, with the result that the plants remained stunted, lacked robustness and fell victims to the disease. In the latter year early growth was vigorous and the roots penetrated the hard pan with the result that the plants were robust and resisted attack. There is, in these observations, corroborative evidence that resistance is the result of a balance between the plant and its environment and that a major problem in such cases is the isolation of a strain which will maintain a healthy condition under the local conditions. The same differential capacity of resistance has been found in Nigeria and Golding (1930) has noted that certain of the selected strains of *Ishan* cotton, a local variety formerly classified under the name of *G. vitifolium*, are markedly resistant.

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SISAL (*AGAVE SISALANA* PERRINE)

Numerous species of the Amaryllidaceous genus *Agave* have an economic use, but the most important of these from the commercial aspect are *A. fourcroydes* Lem., which supplies the *Henequen* hemp of Mexico, also known as *Yucatan sisal, A. sisalana* Perrine, the *sisal*, of which the cultivation has spread so rapidly in East Africa in recent years, and *A. Cantala* Roxb. (not *A. cantula*), the *Maguey* of the Philippines. The two former are sometimes classified as two varieties, *elongata* and *sisalana* respectively, of a single species *A. rigida.*

The sisal plant, like other Agaves, is a perennial which produces a rosette of leaves during a varying number of years and then "poles," that is, sends up a vertical shoot 20 feet or more in height and bare except for small scale-like bracts. The growth of the pole is very rapid, some 6 inches in the twenty-four hours. At the distal end the pole bears numerous lateral branches which, in their turn, bear clusters of flowers ; but abscission takes place, and from the scars left by the shed flowers, numerous vegetatively produced "bulbils" arise. As these develop, they are shed to start an independent life, while the parent plant dies.

The question of economic importance, therefore, concerns the nature of the stimulus causing the plant to pass from the vegetative to the reproductive state. The plant takes some three years to reach the maturity which permits the leaf to be cut ; a period which, combined with the cost of planting up, necessitates a bearing period of several years before poling takes place if cultivation is to be economic. Whether this bearing period is of two to three

years' duration, as is the case in East Africa, or six to ten years, as is common elsewhere, or twenty years, as is reported in the case of *A. fourcroydes* in Mexico, is a matter of vital importance to the industry.

The controlling factor in this matter appears to be climate, and the problem is mainly a physiological one. When the conditions which dictate the passage from the vegetative to the reproductive state are better understood, it may be possible to control and check the tendency to early poling. Work in this direction, as also on the genetic aspect, is in its infancy and has been reviewed by Nutman (1931). The failure of the plant to set fruit creates at once a major obstacle to any genetical attack on the problem. It is, however, an obstacle which does not seem to be insuperable, for, as Nutman has shown, when the main axis of the pole is cut, lateral shoots develop which produce viable seed from which seedlings have been raised at Amani in Tanganyika. The capacity to produce these fruiting laterals appears, however, to be a function of climate, for it only develops at higher altitudes. A detailed account of earlier work in East Africa has been given by Hindorf (1925).

It does not appear improbable that cytological investigation will be found to have a bearing on the practical problem. In the course of his numerous researches into the cytology of the Agaves Catalano (1930) studied *A. sisalana*. He found 14 chromosomes (diploid) in the somatic cells, but in the megaspore great irregularity occurs and some of the phenomena observed are associated with ideas accepted as indicative of hybrid origin. The linking up of this work with the ability of the plant to set viable seed under certain environmental conditions and in response to a particular stimulus has yet to be effected. In hybridization may be found the explanation of those difficulties which beset any attempt at a satisfactory systematic classification and were met with by Drummond and Prain (1906).

A few attempts have been made to inter-cross the various species of *Agave*. Kearney (1918) refers to crosses made by Trabut in Algeria and Vidal (1921) gives an account of crosses between *A. fourcroydes* and *A. sisalana*. With *A. sisalana* as

female parent negative results were obtained, but the reciprocal cross gave fourteen fruits from over 300 flowers crossed and forty-three F_1 seedlings were raised.

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NEW ZEALAND FLAX (*PHORMIUM TENAX* FORST.)

This Liliaceous plant is a native of New Zealand in which country it has long been used by the Maori population as a source of fibre. The main commercial use of the fibre, which is derived from the leaf, is for cordage and binder twine. The source of fibre was originally, and still is, the wild growth of the swampy lands of that country, but in recent years it has been introduced into cultivation and is established as a crop both in New Zealand and Saint Helena. The earliest study of the plant in its agricultural capacity is that of Smerle (1923) and a more extensive study has been commenced by Yeates (1928). The economic forms fall into two species, *P. tenax* Forst. and *P. Cookianum* Le Jolis, but there is a large number of connecting forms, supposed to be hybrids, between these, and specific differentiation must be considered doubtful. Yeates, of whose work only brief accounts have been given, has determined the chromosome number in all cases as 16[1] and all forms appear to be completely inter-fertile. There is a considerable variation in yield of fibre, and in certain forms a blunted leaf apex leads to a lower percentage of short fibres which owe their origin to the running out of lateral strands. The different races can be readily crossed and a considerable range of hybrid plants is now under observation. In a more recent

[1] It is not stated whether this number is haploid or diploid.

publication Yeates (1931) notes that the former idea, that cross-pollination was necessary, is incorrect, and that self-pollination is the rule. This observation is in accord with the frequently observed occurrence of the phenomenon of heterosis.

One of the major questions connected with the cultivation of this plant is the occurrence of the disease known as *yellow leaf*, an obscure disease due apparently to an unidentified virus. Very largely this disease is encouraged by faulty cutting which weakens the plant and renders it susceptible, but there are noteworthy varietal differences in resistance capacity which are under study.

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JUTE (*CORCHORUS spp.*)

The two plants, *C. capsularis* L. and *C. olitorius* L., from which the fibre termed *Jute* is obtained, are Tiliaceous plants of which the cultivation is limited to India and more especially to the north-eastern alluvial tract of that country.

Quality of the commercial product, the fibre, depends largely on the characters length, strength and colour. The former is a character inherent in the plant itself, dependent as it is on the length of the stem ; the two latter characters are to a considerable extent affected by the retting process employed in the extraction of the fibre. From the agricultural aspect length of fibre and yield constitute the characters of dominant importance, but, since the plant is grown in flooded areas, the length of the maturation period to suit the varying duration of inundation is also of importance.

The flowers are small and borne in short cymes carried in the leaf axils. The details of fertilization have been studied by Howard and his associates (1919). The pollen is shed in the bud and the

flower remains open for a short period, some five hours only. Thus self-fertilization is the rule and cross-fertilization a sufficiently rare occurrence to render the isolation of pure races a simple matter. The work expended on such isolation has been briefly described by Finlow (1921). Markedly improved races, both for length of fibre and for yield have been isolated and by 1928, as the result of the organization of the seed supply, over one-third of the jute area was planted up to these.

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CHAPTER XVII

OIL PLANTS

COCONUT (*COCOS NUCIFERA* L.)

THE coconut palm is found throughout the tropics wherever the requisite humidity of the atmospheric conditions prevail. In practice this implies that the palm is only found and cultivated at low altitudes within a short distance of the sea; for here, even at the dryest season, a high atmospheric humidity is maintained. In contrast, the root is very susceptible to stagnant water and a free-drained soil is essential if growth is to be healthy. The uses to which the various parts of the tree are put are innumerable; but, from the commercial aspect, interest centres on the fruit. The outer layer of the pericarp of the mature fruit supplies coir, while within the hard inner layer of the pericarp lies the soft white endosperm which, on drying, forms copra. From this copra oil is extracted. The oil contains stearine and oleine and is used for culinary purposes and in the manufacture of margarine and soap. It is this oil which forms the primary object of the cultivation of the palm.

The coconut is a Cocoine palm which may attain great height and live to a considerable age. Normally the tree commences to flower at about the seventh year, attains its prime at from twenty to forty years and continues to bear in decreasing quantities till its sixtieth or eightieth year. The inflorescence is a spadix borne in the leaf axil, normally one in each axil, and is enclosed by two spathes. Growth of the outer spathe ceases early, but the inner spathe continues to grow until the inflorescence is ready to open, when it splits along one of the longitudinal grooves which mark its surface. The inflorescence is branched, each of the thirty or forty branches carrying a number of sessile flowers. The plant is monœcious with unisexual flowers; the male flowers are numerous

and distributed along the branches and are frequently paired, the female flowers, of which there are rarely more than five on a single branch, are situated at the proximal end of the branches and each carries an opposed pair of male flowers on the same cushion. Dehiscence of the anthers first takes place in the apical flowers and proceeds downwards, and there is a lapse of about a fortnight before dehiscence of the anthers of a single inflorescence is complete. The female flower possesses three nectaries with ducts opening at the apex of the fruit and alternating with the stigmata. When dehiscence of the anthers is completed, the female flowers commence to open; a process which, in like manner, occupies some fourteen days for the single inflorescence and takes place in descending order. During this phase the inflorescence is usually pendent and the nectar extruding from the glands runs on to the stigma. The period of generative activity of the inflorescence, that is, the sum of the male and female phases, is normally less than the interval between the opening of successive inflorescences, and cross-fertilization is, consequently, the rule. Cheesman (1929), quoting unpublished work of Pieris in Trinidad, notes that in that island in no case was an inflorescence observed to open before the female phase of the immediately preceding inflorescence was over, nor was overlapping of the two phases of the same inflorescence observed. The experience of these observers appears to be general (Sampson, 1923); but it is not invariably the rule, for Jack and Sands (1929) record an overlapping of the male and female phases in the dwarf coconut in Malaya. In a later publication Jack (1930) emphasises the relatively homozygous condition found in the dwarf coconut when compared with the commoner tall form.

The original habitat of the coconut palm is doubtful, and Hill (1929) has reviewed the different theories that have been advanced. But, whatever its original home, it is now distributed throughout tropical maritime tracts. The number of varieties has not been accurately determined, partly because of the difficulties inherent in any such determination in the case of a plant of such wide distribution and with so long a life, and partly because of the lack of genetical purity due to the fact that cross-fertilization takes

place normally. Wester (1920) enumerates over eighty names, many of which are, no doubt, synonyms. The most distinct variety, but itself an assemblage of at least three types, is the dwarf coconut of Malaya to which reference has already been made and which Jack and Sands consider to have arisen as a mutation from the tall form. The greater definiteness of the dwarf group appears to be due to the fact that it is commonly self-fertilized. The only investigation of the nuclear constitution of the coconut is that of Santos (1928), who has studied the phases of nuclear division in the pollen mother cells and finds the haploid number of chromosomes to be sixteen.

As would be anticipated, the scope for improvement of the crop is considerable, but owing to the age to which the plant grows, the methods for securing that improvement must necessarily be tedious. Jack and Sands (1922) and Jack (1929a) note that the variation in the number of nuts produced per palm in Malaya has been found to have a coefficient of variation of 34, that 15·5 per cent. of the trees produce 24·5 per cent. of the crop and that 19 per cent. of the trees are uneconomic. Further, and of considerable practical interest, they prove that poor yielders remain poor yielders and high yielders, high yielders. The latter author has reviewed (1929b) the practical aspect of the problem and given an indication of the possible improvement. There is, consequently, ample opportunity for the improvement of the crop by the relatively simple process of the elimination of uneconomic trees on developed estates and of the selection of nuts from heavy bearers for raising young stock for new plantations; the more difficult problem of building up " super " types may well wait. It is a problem which, owing to the absence of genetical purity of the available material together with the time interval between generations, will appal the stoutest-hearted breeder. The earliest work in this direction is of too recent a date to give even an indication of the effect of inbreeding.

Since oil is the dominating economic product, the value of the crop ultimately depends on the yield of oil per unit of cultivation. As long, however, as copra remains the basis of commercial transactions and is valued by appearance, the actual oil content

will remain a secondary question. But, with the post-war tendency to produce oil instead of copra, a feature particularly of the Philippines, the question of oil content cannot be ignored. Work on this aspect is being conducted in Malaya, and Sharples (1930) points out that oil content in nuts as ordinarily picked in estate practice varies from 45 to 75 per cent.; but, since considerable differences exist in different pieces of meat from the same nut and also in the meat from nuts of different degrees of ripeness, the methods of sampling require to be standardized before selection for oil content can be usefully undertaken. An oil content ranging from 63 per cent. in ripe nuts to 72 per cent. in nuts with germinating embryos $3\frac{1}{2}$ inches long has been found, but it has yet to be determined whether this higher oil content in the germinating nut is not counterbalanced by a diminished weight of meat, the result of germination.

Yield of copra remains for the present the primary consideration, and the primary factor here is the capacity of the tree to yield nuts. Here again a difficulty arises in determining the potential yielding capacity of any particular tree. Undoubtedly yield is, in part, determined by the genetic constitution of the tree, but to what extent this is so is difficult to determine owing to the masking action of environmental factors. The drain on the mineral constituents of the soil is considerable. Dash (1929) calculates the plant food extracted per annum per tree in a developed plantation as, potash 37·7 lbs., phosphoric acid 6·11 lbs., nitrogen 52·78 lbs., part of which, however, would be returned if the husks were left on the field. Sampson (1923), as the result of a number of detailed observations on flower and fruit production, while adducing evidence of considerable variability from tree to tree, proves pretty conclusively that a further limitation to yield is imposed by assimilative capacity. Both the number of female flowers in the inflorescence, as well as the number of these which set and mature, is influenced by the number of nuts already ripening; in other words, on the drain on the food supply. There is, further, in these phenomena a seasonal periodicity. Trees of which the inflorescence never carries a large number of female flowers, do not show the same reaction to seasonal change to the

same extent as trees carrying a large number of such flowers. The conditions of growth, therefore, play a primary part in determining the actual yield, and full account must be made for this fact in any endeavour to isolate individuals having an inherent capacity for high yield. Search for characters linked with high yield has not been neglected, and, as Sampson has shown, the leaf scars afford one such character. In heavy bearers it is the assimilative capacity which is the limiting factor, and the carbohydrates are absorbed in the development of the fruit. There is, thus, little reserve for additional vegetative growth, and the interval between successive leaf scars is, in such cases, compressed. Any palm having the leaf scars regularly separated by short intervals may be accepted as a heavy yielder.

In Malaya attention is being directed to the dwarf variety which, owing to the extent to which self-fertilization normally takes place, offers a simpler problem to that offered by the tall varieties. Though the yield per plant of this variety is less than that of the tall variety, the larger number of trees carried per acre, combined with its earlier maturity, more than counterbalances the deficiency. In the case of the tall palm the matter is more complex. Since, in these palms, cross-fertilization is general, not only are trees under cultivation genetically impure, but knowledge of the seed nuts is limited to the female side. The question of artificial fertilization thus assumes importance and the further question of the viability of the pollen arises, since, as has been noted, the female phase is separated by a time interval both from the male phase of the same inflorescence and from the male phase of the succeeding inflorescence. It is known, further, that shed pollen retains its viability for a short period if wetted, a matter of a few hours only. It is unlikely, therefore, that any pollen remains viable in nature over the time interval to the opening of the female flowers. Marechal (1928) and later Pieris (see Cheesman) have studied this question. The work of both investigators indicates that, if kept under suitable conditions, a fair and sufficient percentage of a sample of pollen will retain its viability for sixteen days. Here it is essentially a question of controlled humidity, the optimum conditions being given by

storage over 30 to 40 per cent. sulphuric acid. Marechal, however, claims, as a further condition, that storage in full daylight is necessary. There is, therefore, no insuperable difficulty in the way of self-fertilization by artificial means, and progress can now be made in the raising of palms of known parentage if sterility is not found to accompany the process.

Though the fruit is of major economic importance, certain vegetative characters cannot be overlooked in determining the desirable form of tree. The weight of a well-developed bunch of nuts is considerable, and, if unsupported, the rachis of the inflorescence will tend to buckle with constriction of the vessels and fall of immature fruit as the result of starvation. The natural support of the bunch is the leaf stalk, and a strong leaf stalk, combined with a short inflorescence rachis, forms the most important of the vegetative characters which are desirable.

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OIL PALM (*ELÆIS GUINEENSIS* JACQ.)

This plant, which is a native of the moister areas of tropical West Africa, supplies the Palm Oil of commerce. The major source of supply is the wild growth of the palm in West Africa, but in recent years considerable progress has been made in the establishment of the crop on a plantation basis in the east and especially in Sumatra and Malaya. The plant yields two classes

of oil: one, derived from the pericarp, is an inedible, or semi-edible oil used in the manufacture of soap and candles and as an axle lubricant; the other, derived from the kernel, is edible and used in the manufacture of margarine. After the fruit falls, the pulp, which forms the pericarp, undergoes rapid fermentation with the liberation of free fatty acids, the presence of which detracts much from the commercial value of the oil. An important feature of palm oil production, therefore, is the early extraction of the oil before fermentation sets in and under conditions which destroy the ferment. The preparatory processes must be conducted on the spot and they are, thus, intimately associated with the agricultural aspect of the crop. The oil in the kernel is held under conditions of greater stability and shipment of kernels as such for the subsequent extraction of the oil is the general practice. The production of palm oil, in consequence, presents a dual problem; on the one hand is the purely agricultural problem of the production of a crop, on the other the industrial problem of the production of a standard neutral oil. On the latter point considerable progress has been made in the evolution of efficient machinery suited to the requirements of plantation production, but in West Africa, and especially in the British Colonies, with the wild tree as the source of supply and with an economic system based on individual production in small units, the preparation of a standard product is far from a simple matter. Plantation production, too, offers the freer opportunity for the improvement of the crop, and it is in the east that the greatest strides have been made in the scientific study of this palm.

The Oil Palm, *Elæis guineensis* Jacq., is a Cocoine palm, rarely branching and developing no basal suckers. Propagation, therefore, can only take place by means of seed. The plant is monœcious with unisexual flowers, the male and female flowers occurring as a rule in different spadices, each spadix being enclosed by two spathes, the outer of which bursts early and the inner some two weeks before the flower opens. Hill and Mason (1925) have studied the pollination of the palm and find that, though a periodicity occurs in the production of male and female inflorescences of a single tree, self-fertilization is not ruled out as a

natural phenomenon and is feasible artificially, for pollen will retain its viability up to eighty days under suitable conditions. Bunting and his associates (1927) have studied this periodicity of the two sexes in Malaya and find the male and female cycles to be of three to six months' duration with resting periods of three months. They note, further, that the cycle is not seasonal, for the change takes place at different seasons in different plants. Heusser, in Rutgers' "Investigations on Oil Palms," notes the same periodicity in Sumatra, and, quoting Bücher (1919), assigns the cause to the heritable character of the tree and, perhaps even more, to its nutrition. This subject, and the associated subject of the sex ratio in different trees has been further investigated by Mason and Lewin (1925) who conclude that the main factors differentiating the sex reaction of different trees are probably genetic. Superimposed on this is a population sex ratio having a somewhat regular seasonal periodicity. The flowering cycles are, it is suggested, determined by the relative length of night and day, while the relative importance of the autumn cycle is associated with that major climatic factor of the tropics, rainfall.

The palm commences to flower from four to six years from sowing of the fruit, and this fact, combined with the normal occurrence of cross-fertilization, renders the establishment of even relatively pure strains on a commercial basis particularly difficult. Classification itself, under these circumstances, offers a task by no means easy. Those presented by Chevalier (1910), Beccari (1914) and Yamplosky (*vide* Rutgers) are ultimately based on fruit characters and especially on shell thickness. The latter recognizes four main economic types :—

Var. *macrocarya.* The *Congo* type, with shell about 50 per cent. of fruit weight and pericarp 0·75 to 2·5 mm. thick.

Var. *dura.* The *Deli* type, with shell about 30 per cent. of fruit weight and pericarp 2 to 6 mm. thick.

Var. *tenera.* The *Liscombe* type, with shell about 10 per cent. fruit weight.

Var. *pisifera.* Shell absent, fruit small.

There is, however, ample evidence that trees do not breed true even to these varietal definitions. It is the experience in west

Africa (Smith, 1929) and in Sumatra (Rutgers, 1922). The success of the industry in the latter area appears to be largely due to the fact that the source of material for propagation was, in the first place, a group of four palms growing in the Botanical Gardens at Buitenzorg of which there is reason to suppose that the origin is identical. From these four plants the *Deli* type, characteristic of the Sumatran industry, has arisen. Numerous later importations from West Africa have been made into Sumatra and a full account of these, including an investigation of the history of the *Deli* type has been given by Maas (1923), but, with few exceptions, the palms have appeared economically useless. The F_1 resulting from self- and cross-pollinations from the few selected palms, is only now coming into bearing. A brief account of the work on these as well as on the *Deli* type, is given by Schmöle (1929).

The breeding of a valuable stock aims at the establishment of a heavy yielding type having a thin wall with pericarp rich in oil and a high female to male sex ratio. Considerable difficulty exists in the determination of these characters. Weight of bunch, on which yield largely depends, is influenced in no small degree by the number of fruits fertilized, and it has become customary to resort to artificial pollination, since the location of the female inflorescence within the spathe renders natural pollination not infrequently incomplete. Inherent capacity to yield a heavy crop can only be judged if pollination of all the flowers of the inflorescence is assured. The subject has been studied by Milsum and Greig (1931), who find as the result of artificial pollination a percentage increase of 103. But the matter is not so simple as would appear from the above account. Bunting (1931) has shown that over-pollination is possible when artificial methods are adopted. Probably here, as in the coconut palm, assimilative capacity offers one limiting factor and a tree is unable to develop successfully more than approximately one female inflorescence a month if the flowers of that inflorescence are all pollinated, while, in the life cycle, phases occur when more than one such inflorescence is developed.

The question of the oil content of the pericarp of any particular tree is, similarly, not readily answered, since the measured content

depends not only on seasonal factors, but on the degree of ripening of the fruit. Problems of sampling of no mean order are here involved. The heritable nature of the sex ratio also awaits determination. Progress in the investigation of these matters has been greatest in the east. Waters (1927) has given a detailed account of the Dutch work in Sumatra in the course of which Ferrand has identified external characters which are associated with high yield. These characters include the slow vertical growth of the trunk; a girth above average thickness; leaves long and heavy, drooping towards the outer extremities; a broad, strong leaf base with wide leaf axil and the bunch large. Palms possessing these characters are being used as parents for plantation stock. Work of like nature is in progress at the Pobé station of French West Africa and is described by Houard (1930).

In these areas the establishment of the crop on a plantation basis has facilitated work of this character. In the British Colonies of West Africa where, as has been noted, the economic conditions do not favour plantation development, the work is of a more restricted nature and an account is to be found in *Bull.* 20 *of the Gold Coast Dept. of Agriculture* (1930).

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CASTOR (*RICINUS COMMUNIS* L.)

The castor bean is an albuminous seed derived from the Euphorbiaceous plant, *Ricinus communis* L., probably a native of

Africa, but for long grown throughout tropical and sub-tropical countries. It is, under warmer conditions, a perennial plant, but, at the limits of its range and at high altitudes, it is an annual. It is not very tolerant of cultivation and may become a troublesome weed; it grows best, as in India, in single lines bordering the fields. The commercial product of the bean is an oil, used extensively for medicinal purposes and as an illuminant. In recent years its special suitability for use in internal combustion engines has extended the demand. An account of the character and uses of this oil is given in the Bulletin of the Imperial Institute (1930, 27, p. 30). The plant serves an entirely different function when grown for its leaf which is used in the cultivation of the silk-worm. Certain varieties are also grown as ornamental plants in gardens.

The species, *R. communis*, which is the sole representative of the genus, is very polymorphic and numerous attempts at varietal classification have been made. These have been summarized by Trochain (1930). From the practical aspect two forms are recognized, distinguished by the size of the seed with which difference is associated a difference in oil content, the smaller seed being richer in oil. Oil content, on which the value of the seed depends, is, however, largely influenced by the conditions of growth and the differences so induced are sufficient to mask such inherent varietal differences as undoubtedly exist. Somers Taylor (1921) tested the product of the crop grown from seed having high (average 52·8 per cent.) and low (average 32·9 per cent.) oil content and found the former to average 49·3, and the latter 50·6 per cent. oil. The effect of environmental conditions has been further studied by Gosh (1924). Prisemina (1929), studying the biochemical variability of the seed, found that the yield of oil depends less on geographical factors than on maturity. The amount of free fatty acids varies largely and both this and the lipase content increase as the crop approaches the northern limits of cultivation. These two characters may be taken as a measure of the maturity of the seed. There is, as Sethi (1931) has confirmed, a considerable drop in oil content in seed derived from the lateral branches.

The castor plant is monœcious with unisexual flowers; the terminal inflorescence, whether of the main or subsidiary branches, bearing male flowers below and female above. Varietal differences exist in the inflorescence some of which, such as the relation between male and female flower numbers, have an economic significance. The pollen is shed freely in the morning and retains its viability for at least a week (White, 1923). According to Sethi (1931) pollen is shed between 11 a.m. and 2 p.m. when the maximum temperature is 70° to 80° F. Cross-fertilization is readily effected owing to the separation of the sexes. The extent to which varieties are inter-fertile has not been fully worked out. Popova (1926) hints at a certain reluctance to form natural crosses which he considers to be a means of delimiting sub-species. At the same time the plant is completely self-fertile, and, somewhat surprisingly, considering the separation of the sexes, White (1918a) found that the plant is normally self-fertilized, yielding not more than 5 per cent. of crosses even when conditions appeared most favourable. It is an amount, however, necessitating protective measures when raising pure strains. From the agricultural point of view the percentage of oil is the dominating consideration, but of secondary importance are such characters as acid number, or the quantity of free acid in the oil, method of dehiscence of the seed and age to maturity. Normally the fruit is explosive and the seed liberated with considerable force under the mere influence of drying, but in some varieties the fruit is indehiscent and requires additional labour at harvest.

Few of these characters of economic importance have been studied from the genetic aspect and such study as has been devoted to the plant deals with the more obvious qualitative characters (Harland, 1920, 1921). This neglect is due largely to the fact that the main supply of commerce still comes from India where the plant is chiefly grown along field boundaries and an organized seed supply would be difficult to control. The early attempts to establish it on a commercial basis as a crop in the United States early in the century led to a considerable amount of selection work, especially in Oklahoma (Shaw, 1902).

Little study has been given to the nuclear structure of the

plant, but Tischler (1922) gives the haploid chromosome number as 5. The genetic investigations so far conducted have been summarized by Harland (1928). One case of linkage only has been clearly established, that between the factor for mahogany colour of the stem and leaves and that for light bloom on stem, petioles and capsules. Peat (1928), among other characters, made a preliminary study of the node number to the first inflorescence, a character of economic significance inasmuch as it will affect the maturation period of the plant. He found a definite increase in node number when plants were grown under favourable conditions, a circumstance which must be taken into account when the question of earliness comes to be studied in detail. White (1918b) found heterosis sufficiently strongly marked to suggest the possibility of increasing yield by growing the F_1 cross on a commercial basis; but all crosses did not exhibit the phenomenon and it would be necessary to select suitable parents.

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GROUND-NUT (*ARACHIS HYPOGÆA* L.)

The ground-nut, or pea-nut as it is sometimes called, is a Leguminous plant which is widely cultivated in the tropics and, since it is a short-season crop capable of development in the

summer months, in sub-tropical countries. Its original home appears to be Brazil, and in the area embracing that country are found the twelve species of *Arachis* hitherto recognized. Of these twelve species only three are cultivated, and of these three one only, *A. hypogœa*, has spread throughout the world and is of economic importance.

Chevalier (1929) has given a systematic account of the genus including a tentative varietal classification of *A. hypogœa* based on habit, whether erect or procumbent, fruit shape and size, colour of seed coat and reticulation of the pod. Waldron (1919) divides the species into two sub-species, *fastigiata*, the erect or bunch type, and *procumbens*, the prostrate type. He notes, further, the similarity of the variety *fastigiata* to the wild Brazilian *A. pusilla* Benth., a plant growing in woods and shady places, while var. *procumbens* grows in more open and sandy places and is more definitely xerophytic. From these observations he is led to suggest a dual origin of the cultivated forms, but it must be noted that the two forms cross freely. Badami (1928) alone appears to have investigated the chromosomal constitution of the plant and has found *Spanish* and *Small Japan*, both erect types, to possess 10 chromosomes haploid, while *Virginia*, a procumbent type, has 20. Further, the chromosomal difference is not limited to the number present, for those of *Small Japan* are nearly double the size of those of *Virginia*.

The value of the crop lies in the seed which contains some 45 per cent. oil of high quality suitable for use in culinary work. The seed itself is largely used as a direct food, while the green plant has a value as fodder. From the agricultural aspect the major question is, perhaps, that of yield. But of almost equal importance is the need of a plant which will mature all its fruits simultaneously. This latter need implicates more than one plant character. The erect types are associated with early maturity; the flowers are aggregated round the base of the stem and the fruits not only mature approximately simultaneously, but, owing to their juxtaposition, are readily dug and harvested. The procumbent types are late maturing and the fruits not only mature progressively, but are widely distributed throughout the

soil and hence difficult to harvest. Moreover, there is a marked varietal difference in the seeds according to whether they germinate immediately or pass through a period of dormancy. Types having non-dormant seed and a procumbent habit are the least valuable, for in these the loss which may result from a rain at harvest may be considerable.

The ground-nut is a rapidly growing, erect or procumbent plant, typically leguminous, but characterized by a strongly developed geotropism in the gynophore of the ovary which causes the pod to be buried in the ground, where it ripens. The anatomy, embryology and ecology of the plant have been described by Reed (1924). The flower is typically papilionaceous with a certain amount of irregularity in the stamens and anthers. Three to four flowers are produced in each leaf axil which open successively at intervals of four or five days. The petals unfold about midnight and by the early morning dehiscence of the anthers takes place at which time also the stigma becomes receptive. Self-fertilization appears to be the rule. Subsequent to fertilization the gynophore elongates and buries the ovary which develops underground into a one-, two- or, less commonly, a many-seeded fruit. Emasculation and artificial pollination offer no great difficulty beyond that offered by the low situation of the flower and the habit of burying the pod which necessitates special precautions for the identification of the resultant fruit.

The earliest experimental work on the ground-nut is that of van der Stok (1910), who isolated from each of the varieties studied a number of pure lines, and, in addition, made observations on the progeny of two crosses. Similar work on the isolation of pure strains has been described by McNess (1928) and by Stokes and Hull (1930). Badami (1928) has given a full description of numerous crosses and sums up his work with regard to the characters studied. His conclusions are the following :—

(1) Red seed coat colour; a single factor dominant to brown. In this conclusion he confirms the observations of van der Stok and is confirmed by the work of Stokes and Hull.

(2) Pods ; four groups are distinguished by depth of constriction. He postulates two factors, with cylindrical the double dominant.

(3) Habit; erect is recessive to procumbent with a bi-factorial difference.

(4) Chlorophyll; three factors are concerned with the triple recessive albino and the triple dominant dark green.

(5) Leaves; the cross, leaflets large × small, gives an intermediate F_1 with a wide range in the F_2.

(6) Pod size; at least three factors are concerned, the full dominant having very large pods.

(7) Shell thickness; at least five factors are concerned, the thin shell appears to be linked with the small seed termed by him pygmy.

(8) Shell surface; rough (deeply reticulated) is dominant and at least four factors are concerned.

(9) Stem hairs; hairy is dominant over less hairy, no glabrous form was studied.

(10) Stem colour; a violet tinge is dominant and appears to be associated with hardiness.

(11) Seed number; the many-seeded condition is dominant over one or two seeds, at least three factors are concerned.

(12) Earliness; recessive.

(13) Drought resistance; associated with dark green leaf.

Badami omits any reference to that important character dormancy concerning which Stokes and Hull note that it is an inherent property of the seed incompletely dominant to non-dormancy.

Of suggestive interest in Badami's work is the difference in the behaviour of certain characters for, in some crosses, a character gives a simple mendelian ratio, while, in others, the same character will give rise to a complex series. The suggestiveness of this observation arises from its relation to the difference in chromosomal number which he also observed. It would appear that in future work a chromosomal investigation must accompany genetic investigation. Support may here be found for Waldron's hypothesis of the origin of the cultivated forms.

The only inter-specific cross as yet made within the genus is that between a Spanish strain of *A. hypogæa* and *A. nambyquaræ* made by Stokes and Hull. The F_1 product of the cross appeared

intermediate and fully fertile with complete dominance of the red testa colour and incomplete dominance of the variegation of the seed due to rupture of the testa, characters typical of *A. nambyquaræ*. It is noteworthy that they failed in their attempts to secure the reciprocal cross.

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SESAME (*SESAMUM INDICUM* D.C.)

This widely cultivated plant belonging to the small natural order *Pedaliaceæ* is of uncertain origin and presumed to be African. The extent of its present cultivation ranges well beyond the limits of the tropics as far north as central Asia, where Vaviloff (1931) notes the presence of a very early form. It is widely cultivated in north-east Africa, especially the Sudan, where it passes under the name of *sim-sim*, India, where it is known as *til* in the north and *gingelly* in the south, and as far east as China and Japan. It forms an important crop in Burma, where over a million acres are grown. Whatever its original home, its present cultivation in respect of the major tracts dates from prehistoric times. Being shy of excessive moisture, the seasonal limits are controlled by rainfall as well as temperature.

The plant is a rapidly growing annual commencing to flower three to eight weeks after sowing. The economic value lies in the seed which is used as a source of oil employed in culinary purposes and for perfumes. Despite its wide area of distribution, little attention in the past has been devoted to the study of the varietal differences exhibited. Recently Ram (1930) has studied the

Indian types of which he has classified thirty on a basis of number of flowers in a leaf axil (two to three or one), seed colour, corolla colour and markings and maturation period.

The earliest detailed study of the plant is that of Howard and Khan (1919), who included *Sesamum indicum* among the series of plants of which they studied the details of fertilization. These authors' observations have been repeated and confirmed by Ram. The flowers are borne on long, leafy racemes either singly or in groups of two or three, and open in the early morning. The corolla fades by midday and is shed by the evening. The anthers, the two longer of which lie at the same level as the bifid, irritable stigma, rupture in the bud shortly before the flower opens and at the same time the lobes of the stigma begin to separate and become receptive. The stigma is, thus, covered with pollen at the time the flower opens, and though the flower is, later in the day, visited by insects, self-fertilization appears to be the rule. Howard and Khan, however, note abortion of the stamens as of common occurrence and, in consequence, cases of cross-fertilization are to be found.

The task of isolating selected strains and of the issue of seed of these has been prosecuted in Burma (see reports of the Department of Agriculture, Burma) where one of the major difficulties concerns the occurrence of a sepaloid form in which the petals of some proportion of the flowers become modified to sepals and the flower itself may send out a leafy shoot. Such a sepaloid plant is economically useless as it produces little or no seed. The stimulus towards sepaloidy is undetermined, but Ram has raised from such sepaloid plants offspring showing no trace of sepaloidy which does not appear to be a heritable character. Certain of his observations lead him to suppose that it is an environmental phenomenon emphasised by excessive rainfall.

Little work has been devoted to the genetic analysis of the plant. One character of major economic importance, in that it is associated with habit and especially with maturation period, is root development. Following similar work by Howard and Khan, this has been studied by Ram, who finds two definite types of root formation which are associated with earliness and lateness of

the crop. Abe (1919), in a preliminary study of certain characters studied the branching habit and found it to be allelomorphic to non-branching. Branching is, however, associated with the maturation period and the three characters constitute an inter-linked series of which the inter-relation and genetic behaviour require further investigation. Among the other characters studied by Abe are the glands and the number of locules of the capsule and seed colour. Black seed he found dominant to brown and both dominant to white. A further preliminary study has been made by Nohara (1931).

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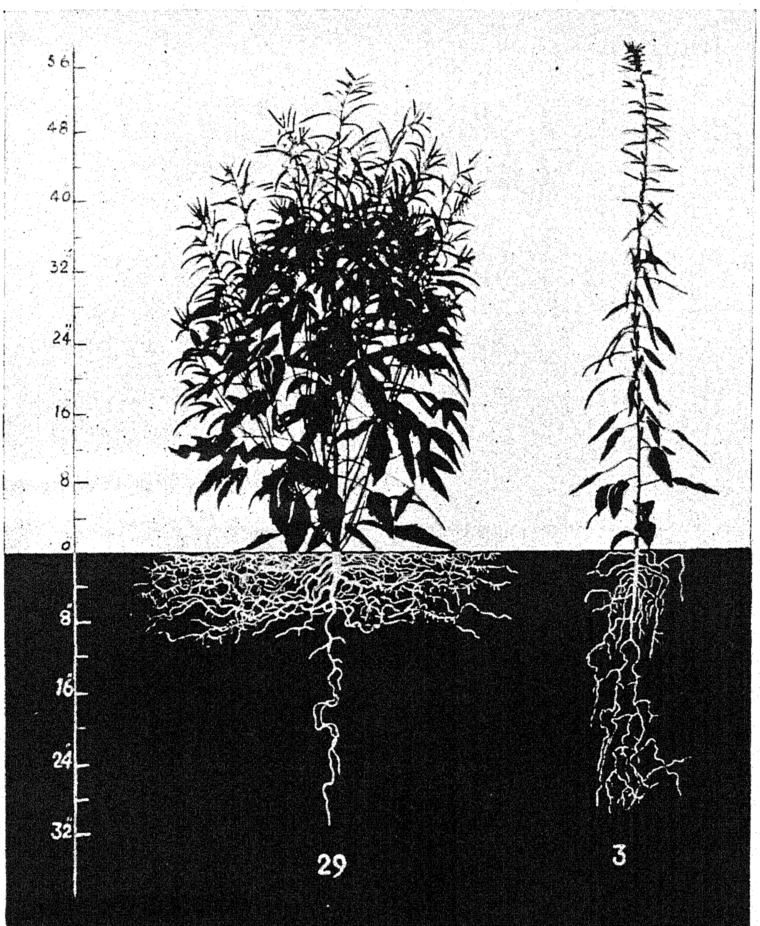
SOY BEAN (*GLYCINE SOJA* SIEB. ET ZUCC.)

The plant, commonly called the soy bean, is an annual belonging to the natural order *Leguminosæ*. Its home is eastern Asia, particularly Manchuria, where it is extensively grown and whence large quantities of seed and seed products are exported. The use of these outside the Orient is of comparatively recent date, but the culture of the plant itself and the consumption of its products in the dietary of the peoples extends back to prehistoric times. The plant is essentially sub-tropical, but its cultivation extends into the tropics on the one hand and as far north as latitude 52° N. on the other and it is capable of withstanding considerable frost when nearing maturity. It is now widely cultivated. In the United States of America, though introduced early in the nineteenth century, its extended cultivation hardly dates before the present century; it has also been cultivated in Europe, Canada, the Argentine, the Philippines and Australia, while, in more recent times it has been introduced into the African colonies.

PLATE XVI



Sesamum indicum D.C. Root development associated with maturation period.

By courtesy of The Secretary of State for India. *Reproduced from "Mem. Dept. Agric., India."*

[*To face p.* 344.

As a consequence of its lengthy history as a cultivated plant and of the fact that early knowledge concerning it was derived through the few early travellers in the Orient, considerable confusion has arisen as to its correct designation. The subject has been discussed in some detail by Piper and Morse (1923). As a further consequence of its extended cultivation in many countries with very varied climatic conditions, it is found in an indefinite number of forms; great confusion exists in varietal terminology, and a situation comparable with that of rice has arisen in which difficulty is found in correlating the results of workers in different countries. The cultivated races are, for the most part, erect and branching, but they appear to be derived from the wild *G. ussuriens* Regel and Maak. Numerous varietal classifications have been advanced, but they necessarily lack phylogenetic significance and are, for the most part, based on fruit and seed characters, the marked vegetative differences of such importance agriculturally being neglected. Reference to the earlier of these classifications is given by Piper and Morse, while Etheridge and his associates (1929) have more recently advanced a classification based on seed colour, flower colour, pubescence, seed shape and hilum character.

The uses to which the soy bean has been put are manifold. In its original home the main use is as human food for which it is prepared in many forms. The green plant may be cut to form most excellent fodder for stock. But its main commercial use is as a source of oil as an illuminant, a substitute for linseed in paints and in the preparation of butter substitutes. Quite recently a movement has developed for its employment, mainly as flour, among the white races of the temperate regions (Ferrée, 1929). The cake, after expression of the oil, is valuable both as a feed and a fertilizer.

The flower of the soy bean is typically papilionaceous, but very small and difficult to handle in artificial fertilization. This difficulty is emphasized by the fact that dehiscence of the pollen takes place in the bud and the flower has been termed, hardly correctly, cleistogamous. As a consequence, self-fertilization is the rule, but the flower is freely visited by insects and occasionally cross-fertilization takes place. The extent of this vicinism has

been studied by Woodworth (1922), who found that when white and purple flowered forms are grown in alternate lines, the percentage of crossed offspring identifiable indicated an actual percentage of 0·16. Garber and Odland (1926) in a similar study, but using slightly different methods of estimation, found a percentage of 0·14 and 0·36 in successive years. Stewart and Wentz (1930), however, found a considerably greater amount of vicinism in the case of the glabrous form to which reference is made below, but this appeared to be due to some abnormality in the pollen leading to delayed fertilization.

In the Orient centuries of cultivation have led to the establishment of numerous local races adapted to the very varied climatic conditions, but, as with most crops raised from an unorganized seed supply, these races lack botanical purity and a considerable amount of work has been devoted to the purification of the crop. Work of this nature has been a feature of many of the experiment stations in America, but Layosa (1918) and Maceda (1919) have conducted similar work in the Philippines and have isolated varieties suited respectively to the wet and dry seasons. Failure of the crop, where such has occurred, has been due mainly to lack of the appropriate organism for the development of the root nodules through which the soy bean, in common with other leguminous plants, procures its nitrogenous requirements. In America the preparation and sale of cultures of the organism have been systematized.

The origin of the large number of variant forms is necessarily undetermined, for their history is lost in antiquity, but evidence exists of the not infrequent occurrence of mutations. Piper and Morse record two apparent cases, while Nagai and Saito (1923) note the origin of a glabrous form in a cross between two pubescent forms and they consider this to be a mutation. A second glabrous form has been reported by Stewart and Wentz (1926) which appears to have a mutational origin. Detailed work connecting such mutational forms with chromosomal structure is lacking.

A considerable literature exists on the behaviour of the more striking characters of the plant when pure races are crossed and a somewhat complex factorial structure has been built up, par-

ticularly for the flower, fruit and seed characters. Purple flower is due to a simple factor, dominant to white, which also develops colour in the vegetative organs. The most interesting of these phenomena, however, concerns the seed colour. This was first investigated by Terao (1918), who found a maternal inheritance of the green cotyledon, and seed coat, colour. The subject has been further investigated by Owen (1927) and Veitch and Woodworth (1929). The transformation of green to yellow in the cotyledons during ripening is due to two dominant factors, either of which develops the yellow colour. In certain varieties, however, there is an additional somatic character, maternally inherited, in the possession of which plants will produce green-seeded offspring when used as the female parent and green or yellow seeded offspring when used as the male parent according to whether they possess or lack the factors for yellow. A further character of interest is that of glabrousness. Certain glabrous forms, like that isolated by Nagai and Saito, appear to be simple recessives to the common pubescent forms, but, in the form isolated by Stewart and Wentz, the glabrous character is dominant.

The genetical constitution of the soy bean has now been worked out in some detail, and Owen (1928) has listed twenty characters of which the relationships are more or less known. Cases of linkage have been recorded and those hitherto identified indicate three linkage groups. Of interest from the economic aspect is earliness which appears to be due to a simple factor linked with the two completely linked factors for black pigment in the seed coat and with the factor for tawny pubescence. Two other characters of economic significance have more recently been studied; Woodworth (1930) gives reason to suppose that the presence of abortive seeds, which may affect 20 per cent. of the total, is due to genetic factors, and Stewart and Wentz (1930) have identified a factor for defective seed coat. From the more general aspect of agricultural adaptability Müller (1930) has studied a number of varietal differences.

The main commercial value of the plant lies in its oil, and efforts have not been wanting to raise the oil content. This figure, as Woodhouse and Taylor (1913) have shown, is variable and depends

in large measure on the degree and conditions of ripening. Quality of oil offers another aspect of improvement. For paints, a drying oil is required, a character which varies inversely with the degree of saturation of the fatty acids. Though the economic value depends on the absorptive capacity with respect to oxygen, the degree of saturation is determined by the capacity to absorb iodine, or the " iodine index." The " iodine index " of soy bean oil is variable, but ranges round 130 as compared with 185 for the most suitable oil for paints, linseed. Cole and his associates (1927) have succeeded, by continuous selection, in isolating races having " iodine indices " of 133·7 and 124·9 respectively; moreover, quality was shown to be independent of quantity. Though the higher of these figures falls much below that of linseed, it is sufficiently high to render the oil a valuable substitute.

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